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BOG FLORA IN THE GRAND RAPIDS, MICHIGAN, AREA: A COMPARATIVE STUDY ACROSS SITES AND OVER TIME— 1901 TO 2017

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ABSTRACT

Michigan's natural landscape includes a diverse assemblage of ecosystems, among the most distinctive of which are peatlands, and more specifically, those known colloquially as "bogs." When botanist Emma J. Cole published the *Grand Rapids Flora* in 1901, she included a large number of bog species documented in the greater Grand Rapids area (16 townships in two counties, an area of 585 square miles). Cole's *Flora* is still the most comprehensive catalog of vascular plants found in West Michigan. This study is part of an ongoing update of Cole's work undertaken by the Calvin University Herbarium to relocate and inventory Emma Cole's collection localities as well as other high-quality natural landscapes in the Grand Rapids region. We compared floristic inventories recently conducted at three bogs in Kent County, all of which are located within the general area covered by Cole's *Flora*, and, to our knowledge, these are the highest quality bogs remaining in this area. Comparing a comprehensive current list of bog plants from these sites with a list of bog plants from *Grand Rapids Flora* provides a rare opportunity to assess floristic change that has occurred in a specified group of plants within a limited geographic area over 120 years of urban and agricultural development. The Floristic Quality Assessment yielded a very high Floristic Quality Index for each of the three bogs studied, signifying that all three sites are significant components of Michigan's native biodiversity and natural landscapes. Sørensen's Index of Similarity indicated a strong similarity among the three bogs to each other, although slightly lower than their even stronger similarity to the historic list of bog plants derived from Cole's *Flora*. The Simple Matching Similarity Index, which compares the site lists with a species pool of potential bog plants, suggests an even stronger similarity among the three bogs (ranging from 72% to 73.1%). A combined current flora of the three bogs compared to Cole's historic list yielded an even higher similarity index of 79.3%. These findings suggest that the three extant bogs, while each exhibiting its own unique flora, have collectively retained a remarkable assemblage of native plants over the past 120 years even while West Michigan experienced significant landscape alteration.

KEYWORDS: Bogs, coefficient of conservatism, peatlands, Emma Cole, Flora of Grand Rapids, floristics, floristic ecology, floristic quality assessment, botanical history, vascular plants, vegetation, similarity indices

INTRODUCTION

Bog Ecology

In North America, the term "bog" generally refers to low nutrient, acidic ecosystems that develop in low lying depressions, typically with a high water

table resulting from little or no inflow or outlets. Bogs in Michigan have been well-studied, particularly in the northern sections of the state. Bog surfaces are usually covered with peat mosses (*Sphagnum* spp.) underlain by fibrous peat and therefore devoid of hard substrate (Rigg 1916; Cowardin et al. 1979). Water that accumulates is almost exclusively from rainfall and water that escapes does so almost exclusively via evapotranspiration. As a consequence of a consistently high water table and acidic conditions, decomposition of biomass is impeded, which contributes to the formation of peat as the substrate. Acidic conditions are enhanced by the metabolism of sphagnum moss, a classic bog indicator (Crow 1969a). These conditions tend to support a characteristic assemblage of plants with high affinity for acidic, peaty substrates, including various insectivorous species such as sundews (*Drosera* spp.), bladderworts (*Utricularia* spp.), and Pitcher Plant (*Sarracenia purpurea*), as well as several very attractive wetland orchids, adding to the bog trotting appeal of these ecosystems. Unique to most bogs is the development of a floating mat of vegetation that grows over the open water from the outer edge towards the center. As the mat matures and expands both horizontally and vertically (as peat is compacted), older peripheral sections can become grounded, while younger areas remain floating. When bog vegetation dies, peat accumulates in the inundated, anoxic conditions under the mat surface. In addition, the outermost zone, or moat, often remains open, at least partly because of the higher nutrient and oxygen content in water along these edges (Crow 1969a; Schwintzer and Williams 1974).

The Michigan Natural Features Inventory program (Cohen et al. 2015) defines “bog” as: “An acidic, nutrient-poor, peat-accumulating wetland that is isolated from mineral-rich water sources by deep peat accumulation and therefore receives most of its water nutrients from precipitation.” In North America, bogs tend to be best developed and most frequent in northern, cold, wet regions, especially within areas that experienced Pleistocene glaciation (Dansereau 1957; Transeau 1905). But peatland formation has occurred widely across the globe where acidic conditions that inhibit decay of vegetable matter are present. For instance, Transeau (1905) notes the considerable development of peaty “southern bogs” along the sandy Atlantic and Gulf Coastal Plain, although these do not typically develop floating mats. In such sites, the genus *Sarracenia* reaches its greatest diversity; only *S. purpurea* ranges northward into glaciated territory (Schnell 2002; McPherson and Schnell 2012). Extensive peatland formation also occurs in the Patagonian region of South America, especially in Tierra del Fuego (Dudley and Crow 1983). Additionally, Ritter and Crow (2005) reported on a small bog with a floating sphagnum mat in a Bolivian cloud forest, which clearly fits within the broad definition of “bog.”

While bog surface topography is visually flat, bog mats are mosaics of microhabitats and therefore sustain a surprisingly high diversity of species. This diversity is supported by slow succession over time, as bog mats extend over open water and as older sections become grounded when peat build-up contacts the underlying mineral soils. In southern Michigan, the central area of a bog will usually have an open water zone where aquatic species such as white and yellow water lilies (*Nymphaea odorata* subsp. *odorata*, *Nuphar advena*), pondweeds (*Potamogeton* spp.), Watershield (*Brasenia schreberi*), and blad-

derworts (*Utricularia* spp.) can be found, at times accompanied by emergent aquatics such as Pickerelweed (*Pontederia cordata*) and Arrowhead (*Sagittaria latifolia*). The floating mat zone is usually structurally composed of sedges, such as *Carex lasiocarpa*, *Carex oligosperma*, and Twig-rush (*Cladium mariscoides*). Succession often leads to the development of a fairly large Leatherleaf (*Chamaedaphne calyculata*) zone behind, or adjacent to, the sedge mat. A shrub zone of woody species such as Michigan Holly (*Ilex verticillata*), Mountain Holly (*Ilex mucronata*), Chokeberry (*Aronia prunifolia*) and Poison Sumac (*Toxicodendron vernix*) can often be found forming toward the outer portion of this floating mat. The outer zone of the bog is typically dominated by a dense growth of woody species, including Highbush Blueberry (*Vaccinium corymbosum*), Tamarack (*Larix laricina*), and/or Black Spruce (*Picea mariana*) (Dachnowski 1908; Crow 1969a; Hellquist and Crow 1999). Sphagnum moss or peat moss is a consistent ground substrate throughout most of these zones, represented by multiple species of *Sphagnum*, depending on microhabitat (Hellquist and Crow 1999). Because bogs are home to suites of rare or specialized plants, including orchids and insectivorous plants (Dachnowski 1908), many botanists, including Emma J. Cole, have been drawn to study the vegetation of these intriguing ecosystems.

Peatlands in Grand Rapids

Highly-regarded as a teacher and scientist, Emma J. Cole was well known among botanists for her *Grand Rapids Flora: A Catalogue of the Flowering Plants and Ferns Growing without Cultivation in the Vicinity of Grand Rapids, Michigan* (Cole 1901; see also Crow 2017; Stivers and Crow 2018). Although this book was published more than a century ago, it remains the most comprehensive study of the flora of the Grand Rapids area. Since 1901, considerable changes have occurred in the Grand Rapids area that have greatly influenced the land use, and thereby the botanical diversity, in this region. Cole (1901) listed the flora of numerous natural areas in the vicinity of Grand Rapids. Peatlands (both bogs and fens) were among the habitats that she frequented, an interest that possibly emerged from her childhood in Vergennes Township, as her home was within 0.5 mile of Miller's Lake Bog, a small bog of only 9 acres that persists today and is included in this study.

However, not all the bogs that Cole visited remain. For example, Cole (1901) described the 500-acre Burton Street Swamp (Figure 1) on the southwest side of the city, a peaty site with both fen and sphagnous bog habitat locally referred to as "Orchid Swamp," boasting such orchids as: Putty-root (*Aplectrum hyemale*), Arethusa (*Arethusa bulbosa*), Grass-pink (*Calopogon tuberosus*), Small White Lady's-slipper (*Cypripedium candidum*), the large and small Yellow Lady's-slipper (*Cypripedium parviflorum*, both var. *parviflorum* and var. *makasin*), Showy Lady's-slipper (*Cypripedium reginae*), and Club-spur Orchid (*Platanthera clavellata*). During the proofing of Cole's galley sheets in 1900, Luther Livingston, a former Grand Rapids student and her valued proof-reader for the *Flora*, sent her a letter with notes reminiscing about his treks to the Burton Street Swamp. Referring to Arethusa (*Arethusa bulbosa*), he said: "We gathered them



FIGURE 1. Left: Portion of map from Emma Cole's *Grand Rapids Flora* (1901) showing location of Burton Street Swamp (Orchid Swamp) just southwest of the City of Grand Rapids. Right: The current landscape via Google Earth showing the expansion of development in the surrounding area. The outlined portion indicates the outline of Orchid Swamp then and now.

every spring [1882–1886] as long as I was in G. R. They grew in the soft mounds or cushions of living sphagnum, never were very abundant but, I presume we have gathered 30 flowers in a season” (Stivers and Crow 2018). The rare Orange Fringed Orchid (*Platanthera ciliata*), now state-endangered, was also known from this locality. The Orchid Swamp was later drained and, regrettably, the area became occupied by residential housing, commercial development, and a large General Motors stamping plant. A similar fate was met by Diamond Street Swamp, which was another valued site for the rare Orange Fringed Orchid (*Platanthera ciliata*); the area is now occupied by residential housing, and no hint of the former beautiful peatland remains.

Even in Emma Cole's day, draining of wetlands was commonplace. She specifically mentioned that the Saddle-Bag Swamp, then 5 miles east of the city in Grand Rapids Township, had been drained and burned in 1895 (Cole 1901). She reported that Saddle-Bag Swamp, a site for Pink Lady's-slipper (*Cypripedium acaule*), Green Adder's-mouth (*Malaxis uniflora*), White Fringed Orchid (*Platanthera blephariglottis*), Prairie Fringed Orchid (*P. leucophylla*) and Green Fringed Orchid (*P. lacera*), had been destroyed in 1895 after being drained and burned. This 1000-acre peatland system once included seven lakes: East Lake (previously Bailey Lake), Carmody Lake, Frawley Lake, Swamp Lake, the two Twin Lakes, and Echo Lake (previously Webster Lake)—all “formerly surrounded by open sphagnum bogs which gradually passed into sphagnum swamp, overgrown with tamarack, black spruce, mountain holly, leatherleaf, and huckleberry” (Cole 1901). These lakes have become magnets for lakefront housing and today are mostly surrounded by year-round residences. Additionally, the areas immediately adjacent to Twin Lakes support two landscaping companies,

and large quantities of peat have been harvested for horticultural purposes. Recently, conflict arose when the developer of a multi-million dollar residential project claimed that one of the landscape companies, in business since 1957, creates noise pollution (stone/concrete crushing) and would be a hazard to residents due to large trucks and equipment used in the business (Herring 2018). Thus, human impact on the once wonderful Saddle-Bag Swamp has been, and continues to be, significantly detrimental.

Even though many of the habitats Emma Cole (1901) described have been lost, the account Cole recorded in her *Grand Rapids Flora*, as well as the many specimens documenting the *Flora* (see Crow 2017), have nevertheless served as an excellent record of plants that she observed from various natural areas, including several bogs that were present in the Grand Rapids region in the 1890s, some of which do still remain. This study describes and compares three rather high-quality bogs and evaluates a combined inventory of these three locations in relation to a list of bog species generated from Cole's *Flora* (1901) augmented by extant historical specimens in the University of Michigan Herbarium (MICH) and the Michigan State University Herbarium (MSC). Our comparison across more than a century provides a rare opportunity to assess changes in bog flora in the Grand Rapids area, thereby shedding light on the botanical and ecological impact of urban and agricultural development that has occurred in this region.

MATERIALS AND METHODS

Botanical Inventory

During the summers of 2015 through 2019, numerous selected sites have been inventoried as part of the Emma Cole Grand Rapids Flora Project conducted by faculty and students through the Calvin University Herbarium. The aim of this project is to visit as many of the locations described by Cole (1901) as possible, comparing their present-day status with her 1901 descriptions. We also visited and evaluated other high-quality natural areas in the Grand Rapids region that were not mentioned by Cole, but that we encountered while doing this work. Sites visited in the comparative study reported in this paper are three bogs: Saul Lake Bog (inventoried in 2015), Dead-lake Bog (inventoried in 2017) and Miller's Lake Bog (inventoried in 2015 and 2018); only Miller's Lake Bog was known to Cole. Descriptions of the vegetation were recorded and voucher specimens were collected to document the flora of each bog, with the first set retained in the Calvin University Herbarium (CALVIN). Duplicate specimens were deposited at MSC and MICH. Plant identifications were made using a variety of references, but especially relying on *Field Manual of Michigan Flora* (Voss and Reznicek 2012) and MICHIGAN FLORA ONLINE (2011), which were also our standards for botanical nomenclature.

Study Sites

Dead-lake Bog (42° 46.284' N, 85° 37.260' W)

The locality we have called Dead-lake Bog is an otherwise un-named peatland within Gaines Township, Kent County, located just north of 108th St. and just west of Kalamazoo Ave. SE, situated along the northern edge of the Kent–Allegan County line (Figure 2). Dead-lake Bog is adjacent to a large, active sand and gravel pit on the northwest, and bordered on the other sides by agricultural land. This bog was apparently unknown to Emma Cole, although it is within the district of 16 townships covered by her *Flora* (Cole 1901). The outer portion of this bog is dominated by tall shrubs such as Silky Dogwood (*Cornus amomum*), Michigan Holly (*Ilex verticillata*), Buttonbush (*Cephalanthus occidentalis*), Tamarack (*Larix laricina*), and Highbush Blueberry (*Vaccinium corymbosum*). Poison Sumac (*Toxicodendron vernix*) occurs scattered in the more open portion of the shrub zone. Large patches of Leatherleaf (*Chamaedaphne calyculata*) dominate various portions of the bog mat;



FIGURE 2. Google Earth image of Dead-lake Bog.

the common bog sedge (*Carex lasiocarpa*) forms patterned zones in some areas, while a different bog sedge, *Carex oligosperma*, is dominant in other areas; an additional relatively large patch dominated by Hard-stem Bulrush (*Schoenoplectus acutus*) is also present. Another common sedge, Twig Rush (*Cladium mariscoides*), grows widely, somewhat scattered across the bog mat, especially among the *Carex* species. Large-berried Cranberry (*Vaccinium macrocarpon*) and Small-berried Cranberry (*V. oxycoccos*) also tend to be associated with the sedge-dominated zones, along with four carnivorous species, Pitcher Plant (*Sarracenia purpurea*), Round-leaved Sundew (*Drosera rotundifolia*), Spatulate-leaved Sundew (*D. intermedia*), and Flat-leaved Bladderwort (*Utricularia intermedia*). While no singular central bog pond exists, there are a few scattered areas of aquatic pools, one of which is surrounded by a dense population of Beak-rush (*Rhynchospora fusca*). These open water zones and the occasional channels between them tend to be populated by White Waterlily (*Nymphaea odorata* subsp. *odorata*) and Yellow Pond-lily (*Nuphar advena*); Horned Bladderwort (*Utricularia cornuta*) and Small Bladderwort (*U. minor*) can also be found growing in the still waters of the pools.

Saul Lake Bog (43° 3.957' N, 85° 24.870' W)

This bog is located in Grattan Township, ca. three miles east of the village of Cannonsburg on 6 Mile Rd., and 0.5 mile north on a long private gravel road or driveway (Figure 3). It lies slightly less than one mile east of the specific area covered by the map in Cole's (1901) *Flora* and was likely unknown to her. About 75% of the peatland is owned by the Land Conservancy of West Michigan as part of their Saul Lake Bog Preserve. The sphagnum bog is surrounded by a moat and an outer shrub community with an abundance of Buttonbush (*Cephalanthus occidentalis*), Dwarf Birch (*Betula pumila*), Red Maple (*Acer rubrum*), High-bush Blueberry (*Vaccinium corymbosum*), and an occasional Black Gum (*Nyssa sylvatica*). The characteristic bog conifer zones are occupied by both Tamarack (*Larix laricina*) and Black Spruce (*Picea mariana*). As with Dead-lake Bog, there is no clearly defined central bog pond, although large portions of the northern section of the bog mat have extensive aquatic pools and channels of water. These small open water habitats contain White Waterlily



FIGURE 3. Google Earth image of Saul Lake Bog.

(*Nymphaea odorata* subsp. *odorata*), Yellow Waterlily (*Nuphar advena*), Water-shield (*Brasenia schreberi*), Oakes' Pondweed (*Potamogeton oakesianus*), and three carnivorous bladderworts (*Utricularia gibba*, *U. vulgaris*, and *U. cornuta*). The sedge-dominated zones (*Carex lasiocarpa*, *Cladium mariscoides*) are host to Small- and Large-berried Cranberry (*Vaccinium oxycoccos*, *V. macrocarpon*), carnivorous sundews (*Drosera intermedia*, *D. rotundifolia*), Tawny Cottongrass (*Eriophorum virginicum*), Beak-rush (*Rhynchospora alba*), and occasional patches of Bog Rosemary (*Andromeda glaucophylla*) and Bog Buckbean (*Menyanthes trifoliata*). Over 1000 individuals of the Rose Pogonia orchid (*Pogonia ophioglossoides*) were observed growing in the open sedge zones. As is characteristic of many bogs, Leatherleaf (*Chamaedaphne calyculata*) is dominant in large patches, forming a low, dense shrub thicket where little else grows.

Miller's Lake Bog (42° 57.800'N, 85° 24.500'W)

Miller's Lake Bog is a bog in Vergennes Township on the east side of Parnell Ave. NE, 0.6 mi. south of Bailey Drive NE and 0.4 mi. north of Vergennes St. NE (Figure 4). It appears to be a classic, although quite small, kettlehole bog, that is, a bog with no inlet or outlet, but with a typical outer moat surrounding the bog. Immediately inside the moat a tree and shrub zone occur, with Red Maple (*Acer rubrum*), Highbush Blueberry (*Vaccinium corymbosum*), Michigan Holly (*Ilex verticillata*), Mountain Holly (*I. mucronata*), and Black Chokeberry (*Aronia prunifolia*). Poison Sumac (*Toxicodendron vernix*) is common toward the inside of the shrub zone and scattered on the older portion of the bog mat. Leatherleaf (*Chamaedaphne calyculata*) forms large colonies on the bog mat that are accompanied by very few other species within its dense stands. A rather extensive sedge mat dominated by *Carex oligosperma* occurs on the southwest side of the bog and as narrow strips between the



FIGURE 4. Google Earth image of Miller's Lake Bog.

extensive Leatherleaf zone of the east side and the outer shrub zone. Although *Carex lasiocarpa*, perhaps one of the most characteristic of bog sedges, does occur in the bog, its presence is extremely sparse (in contrast, *Carex lasiocarpa* is the dominant graminoid at Saul Lake Bog, where *Carex oligosperma* was not found). A small pond (1.17 hectares, 2.89 acres) occupies the central portion of Miller's Lake Bog and is unusual in having a dense shrub zone immediately on the margin of the floating mat (Figure 4). Of some concern, Glossy Buckthorn (*Frangula alnus*), a non-native and aggressive shrub, has infiltrated the bog, although it is currently represented by only scattered individuals. Aquatic plants occupy the margin of the pond, dominated by Yellow Waterlily (*Nuphar advena*), with the submergent Common Bladderwort (*Utricularia vulgaris*) and softwater Spiny Coontail (*Ceratophyllum echinatum*), a species seldom encountered in Michigan. Interestingly, this bog has neither Tamarack (*Larix laricina*), which is typical in Michigan bogs, nor Black Spruce (*Picea mariana*), the other boreal conifer species that occurs only sporadically in bogs of southern Michigan (as in Saul Lake Bog). It should be noted that in Kent County Black Spruce is close to its southern geographical limit (Spei and Kashian 2018), although Tamarack extends further south into northern Illinois and northern Indiana (USDA, NRCS 2020).

This bog is located less than 0.5 mile from Emma Cole's childhood home and within the 9 sections (9 square miles) of Vergennes Township that Cole (1901) extended eastward from her district of 16 townships. This small bump-out on her map was extended because Cole had made so many collections pertinent to her *Flora* near her family home (see map in Crow 2017). The bog is an ecological jewel and may well have been a favorite locality that whetted Cole's appetite for botanical studies, harboring interesting orchids and carnivorous plants.

Floristic Quality Assessment

We compiled a plant species list for each site for use in making floristic quality assessments. From these lists we generated Floristic Quality Index (FQI) values for each site using the online Uni-

versal FQA Calculator (<https://universalfqa.org>) based on the Michigan Floristic Quality Assessment Database–2014 (Reznicek et al. 2014; Freyman et al. 2016). This assessment tool is based on assigning each native Michigan species a Coefficient of Conservatism (C), ranging from 0–10. This C value reflects a given species' fidelity to undisturbed habitats, in which a higher value indicates greater fidelity. After calculating the Mean C (\bar{C}) for each site inventoried, which is the average of the coefficients of conservatism of the species in that site, a Floristic Quality Index (FQI) for the site is calculated as follows:

$$\text{FQI} = \bar{C} \times \sqrt{n},$$

where n is the number of native species in the site. Plants with C values of 8–10 indicate a very strong affinity to a narrow range of undisturbed ecological conditions, whereas C values of 0–2 are associated with more widespread disturbance-tolerant species that can be found growing in a wide range of habitats. Hence, the Floristic Quality Index provides a reliable indication of the natural quality of an area and can be used to compare the ecological integrity of different landscapes (Bried et al. 2013). The Universal FQA Calculator generates a Native FQI and a Total FQI, the former based only on the native species present at the locality inventoried, whereas the Total FQI includes non-native species (each assigned a C -value of 0, thus lowering the overall FQI value), and giving a comparative indication of the impact of non-native species on a site's floristic quality.

Present-day Bog Flora vs. Historical Bog Flora

To assess the present-day floristic composition of bogs in the Grand Rapids area in comparison with that of the 1890s, we compiled a list of species from Cole's (1901) *Flora*. But, because Cole's purpose was to compile a comprehensive account of all the species growing in the Grand Rapids area, she did not conduct full inventories of specific sites she visited. Rather, in her *Flora*, she recorded general descriptions of what she considered to be significant sites, providing us with a sense of the historical quality of these locations. She also highlighted especially interesting landscape features, as well as individual species. Thus, to compile a "historical catalog of bog plants" we chose species Cole described as having been collected in a bog, or in a boggy, or sphagnum habitat. We also included species that, based on their attributes, had a high probability of having been collected in a bog. Species indicated in *Grand Rapids Flora* as occupying fens, but not bogs, were excluded from the list. To compare our results with the compiled list of Cole's bog plants, we combined the present-day floristic lists of the three bogs into a single bog flora list. For further analyses utilizing the Simple Matching Index method (Mueller-Dombois and Ellenberg 1974), we also generated a larger "species pool" (described below) of West Michigan bog plants.

Similarity Index

We used the Sørensen Index of Similarity (Mueller-Dombois and Ellenberg 1974) to compare the flora among each pair of the bogs studied; we also used the Sørensen Index to compare the combined list of present-day bog plants with the historical bog species of Emma Cole's *Flora* (1901). This comparison allowed us to evaluate whether these lists are effectively describing the same habitat type. The Sørensen Index comparing two habitats (or lists) is calculated as follows:

$$\text{Sørensen's Index} = [2C \div (A+B)] \times 100,$$

where A and B are the numbers of species in the two habitats (or lists), respectively, and C is the number of shared species between the two habitats (or lists).

A second index of similarity, the Simple Matching Index (Mueller-Dombois and Ellenberg 1974), was employed to evaluate the similarity of species composition between the list of historical bog species of Cole (1901) and our combined bog inventories taken in 2015–2018. The Simple Matching Index is calculated as follows:

$$\text{Simple Matching Index} = [(a+d) \div (a+b+c+d)] \times 100,$$

where a is the number of species present in both time periods, b is the number of bog species in the 1890s, c is the number of species present at our three sites, and d is the number of species from both time periods that are absent from a potential "species pool" (defined below) (Mueller-Dombois and El-

lenberg 1974). While some indices, such as the Sørensen’s Index, measure the species held in common between two locations (or two time-frames), the Simple Matching Index goes further and considers the number of species *not* present within the floras of each time-frame (in our use of the index). This is done by comparing the lists to a larger potential species pool generated from a regional list of possible species that could reasonably be present at these particular sites (Bradley, 2005; Bradley and Crow 2010), thereby indicating the strength of the similarity in a broader regional context.

The West Michigan “species pool,” consisting of 166 taxa that could potentially become established in any bog habitat within the area, was generated from a compilation of bog species included in Cole’s (1901) *Flora* (the historic bog flora list), all the species from our fieldwork conducted in the three bog sites described here, and bog species from other published accounts within the Grand Rapids area, such as inventories conducted by Van Dragt et al. (2005) and Warners et al. (2007). We further expanded the species pool for West Michigan by consulting the Flora of Kalamazoo County (McKenna 2004) for species known to occur in bogs, by including species listed for Pennfield Bog, Calhoun Co. (Crow 1969b), and by adding species from unpublished field work by Crow in three bogs of Kalamazoo County. Further, we searched MICHIGAN FLORA ONLINE (2011) for species with labels that indicate “bog” as the habitat for Allegan, Barry, Berrien, Branch, Cass, Ionia, Kent, Ottawa, Montcalm, Muskegon, Newaygo, St. Joseph, and Van Buren Counties. Some species added from our recent field work represent new county records for Kent County. However, species of peaty habitats that tend to be characteristic of calcareous sites, such as fens, but not acidic boggy sites, are excluded from the species pool.

RESULTS AND DISCUSSION

Floristic Quality Assessment of Present-day Bogs

Large areas of Michigan’s landscape have changed significantly from their pre-settlement vegetation as a consequence of logging, widespread landscape modification, and urban growth. Hence, Michigan’s native biota has become restricted to relatively small, isolated tracts of natural landscapes, which have been impacted indirectly through hydrological alterations as well as edge effects. Truly representative pre-settlement ecosystems are rare elements of the West Michigan landscape today. The Michigan Floristic Quality Assessment system was developed to aid in evaluating the significance of natural habitats with respect to Michigan’s native biodiversity and natural landscapes (Herman et al. 2001). Table 1 summarizes the overall Floristic Quality Assessment metrics for the bog localities studied.

TABLE 1. Summary of Floristic Quality Assessment metrics for all bog floras studied.

Bog Flora	Hectares	Total FQI	Native FQI	Mean C (standard error)	Total Species	Native Species	Non-Native Species
Historical Bog Flora based on Cole (1901)	n/a	71.5	72.4	6.0 (0.2)	142	141 (99.3%)	1 (0.7%)
Dead-lake Bog	36.92	49.7	51.3	5.7 (0.2)	76	73 (96.1%)	3 (3.9%)
Saul Lake Bog	22.1	53.7	54.7	6.2 (0.2)	75	73 (97.3%)	2 (2.7%)
Miller’s Lake Bog	3.68	49.2	50.2	5.8 (0.2)	72	70 (97.2%)	2 (2.8%)
Combined present-day bog flora	62.7	64.1	65.2	5.8 (0.2)	122	118 (96.7%)	4 (3.3%)

Dead-lake Bog

Dead-lake Bog occupies an area of 36.92 hectares (91.22 acres) (Figure 2). The bog has a species richness of 76, of which 96.1% of the species are native (only 3 species are non-native); 22 species (29%) have a *C* value of 8–10, of which 12 species show an extremely high fidelity to pristine conditions (*C* value of 10) (Tables 1 and 2). The Mean *C* for the site is 5.7, the Native FQI is 51.3, and the Total FQI is just slightly lower at 49.7, which reflects the near absence of adventive species. According to Herman et al. (2001), any site with a Native FQI score of 50 or higher is valued as a significant component of Michigan's native biodiversity and natural landscapes.

Of particular interest at Dead-lake Bog was the discovery of a new county record for Kent County, Beak-rush (*Rhynchospora fusca*), and two species that had not been documented in Kent County since the 1890s: Arrow-grass or Pod-grass (*Scheuchzeria palustris*) (collected by Cole in 1891, 1894, and 1897) and Fen Willow-herb (*Epilobium leptophyllum*) (collected by Cole in 1896, 1898, 1899, and 1899, and by Skeels and Shaddick in 1896), according to MICHIGAN FLORA ONLINE (2011).

Saul Lake Bog

Saul Lake Bog (Figure 4), a 22.1-hectare (54.61 acres) peatland, a favorite Calvin University taxonomy class field trip site, was inventoried in 2015 adding to earlier specimens collected beginning in 2000 by various visitors. Overall, this site has the highest FQI values of the three bogs studied (Table 1). Saul Lake Bog has a species richness of 75, of which 97.3% are native species (only two species are non-native) (Table 1). A total of 26 species (36%) have a *C* value of 8–10, 12 of them showing an extremely high fidelity to undisturbed habitat with a *C* value of 10 (Table 2). The Floristic Quality Assessment calculated a Mean *C* of 6.2 for the site, a Native FQI of 54.7 and a slightly lower Total FQI of 53.7, making this another site with a score of 50 or higher, thus considered to be a significant component of Michigan's native biodiversity and natural landscapes.

Of particular interest was the discovery of two new county records for Kent County (Table 3), both species having a *C* value of 10: a diminutive Cottongrass (*Eriophorum tenellum*) and a soft-water, floating-leaved pondweed (*Potamogeton oakesianus*). Pipewort (*Eriocaulon aquaticum*), with a *C* value of 9, occupies the wet channels and pools and was found growing only in this bog among our recent inventories. This species has been documented from only 2 other localities in the area, one of which was Emma Cole's collection in 1899 from a location ca. 2 miles away, Bostwick Lake in 1899, and the other collected by her in 1896 at Pine Island Lake (now Little Pine Island Lake) ca. 10 miles westward in Plainfield Township. Another species of wet channels and pools in this bog is Yellow-eyed-grass (*Xyris difformis*), with a *C* value of 8, which had not been documented from Kent County since 1940 (Table 3); this species is also well-represented in Dead-lake bog. Our collection of Grass-pink (*Calopogon tuberosus*), with a *C* value of 9, was the first documentation of this beautiful orchid in Kent County since 1939 (MICHIGAN FLORA ONLINE 2011).

TABLE 2. Taxa having a *C* value of 8–10, indicating a high level of fidelity to a narrow range of undisturbed ecological conditions. An X indicates the presence of a taxon in that flora.

Taxon	<i>C</i> Value	Cole's <i>Flora</i>	Dead-lake Bog	Saul Lake Bog	Miller's Lake Bog
<i>Andromeda glaucophylla</i>	10	X	X	X	X
<i>Arethusa bulbosa</i>	10	X			
<i>Calla palustris</i>	10	X		X	
<i>Carex limosa</i>	10	X			
<i>Carex oligosperma</i>	10	X	X		X
<i>Carex pauciflora</i>	10	X			
<i>Carex tenuiflora</i>	10	X			
<i>Ceratophyllum echinatum</i>	10				X
<i>Cladium mariscoides</i>	10	X	X	X	
<i>Drosera intermedia</i>	10	X	X	X	
<i>Eriophorum augustifolium</i>	10	X			
<i>Eriophorum gracile</i>	10	X			
<i>Eriophorum tenellum</i>	10			X	
<i>Eriophorum vaginatum</i>	10	X			
<i>Platanthera blephariglottis</i>	10	X			
<i>Platanthera ciliaris</i>	10	X			
<i>Platanthera flava</i>	10	X			
<i>Pogonia ophioglossoides</i>	10	X	X	X	X
<i>Potamogeton oakesianus</i>	10			X	
<i>Sarracenia purpurea</i>	10	X	X	X	X
<i>Scheuchzeria palustris</i>	10	X	X		X
<i>Triadenum virginicum</i>	10	X	X		X
<i>Utricularia cornuta</i>	10	X	X	X	
<i>Utricularia intermedia</i>	10	X	X	X	
<i>Utricularia minor</i>	10	X			
<i>Utricularia purpurea</i>	10	X			
<i>Vaccinium macrocarpon</i>	10	X	X	X	X
<i>Woodwardia virginica</i>	10	X	X	X	X
<i>Xyris torta</i>	10	X			
<i>Calopogon tuberosus</i>	9	X		X	
<i>Carex trisperma</i>	9	X	X	X	X
<i>Eriocaulon aquaticum</i>	9	X		X	
<i>Nyssa sylvatica</i>	9	X		X	X
<i>Salix candida</i>	9	X			
<i>Carex canescens</i>	8	X	X		
<i>Carex lasiocarpa</i>	8	X	X	X	X
<i>Chamaedaphne calyculata</i>	8	X	X	X	X
<i>Dulichium arundinaceum</i>	8	X	X	X	X
<i>Eriophorum virginicum</i>	8	X	X	X	X
<i>Glyceria canadensis</i>	8	X	X	X	X
<i>Malaxis unifolia</i>	8	X			
<i>Menyanthes trifoliata</i>	8	X		X	X
<i>Nuphar advena</i>	8	X	X	X	X
<i>Pontederia cordata</i>	8	X			
<i>Rhododendron groenlandicum</i>	8	X			
<i>Salix pedicellaris</i>	8	X			
<i>Utricularia geminiscapa</i>	8	X			X
<i>Utricularia gibba</i>	8	X		X	X
<i>Vaccinium oxycoccos</i>	8	X	X	X	X
<i>Viola blanda</i>	8	X			
<i>Xyris difformis</i>	8		X	X	

TABLE 3. Additions to the bog flora of the greater Grand Rapids area since Cole’s (1901) *Flora*, including new county records for Kent County, with voucher specimens and herbarium acronym.

Taxon	County Record	Locality	Documenting Specimens
<i>Carex atlantica</i> subsp. <i>capillacea</i>	X	Dead-lake Bog Saul Lake Bog	<i>Van Donselaar, Antuma, Quakenbush & Warners EC-17-2290</i> (CALVIN, MICH) <i>Leisman, Van Staalduinen & Warners EC-15-183</i> (CALVIN)
<i>Ceratophyllum echinatum</i>	X	Miller’s Lake Bog	<i>Chum & Crow EC-18-3145</i> (CALVIN, MICH)
<i>Eriophorum tenellum</i>	X	Saul Lake Bog	<i>Crow 10695</i> (CALVIN, MICH) <i>Leisman, Van Staalduinen & Crow EC-15-510</i> (CALVIN, MICH)
<i>Frangula alnus</i> (adventive)		Dead-lake Bog Miller’s Lake Bog	<i>Van Donselaar, Antuma, Quakenbush & Warners EC-17-2282</i> (MICH, CALVIN) <i>Lindemulder & Van Donselaar EC-18-3565</i> (MICH, CALVIN)
<i>Lycopodiella inundata</i>	X	Saul Lake Bog	<i>Leisman, Van Staalduinen & Crow EC-15-504</i> (CALVIN)
<i>Potamogeton oakesianus</i>	X	Saul Lake Bog	<i>Leisman, Van Staalduinen & Crow EC-15-512</i> (CALVIN)
<i>Rhynchospora fusca</i>	X	Dead-lake Bog	<i>Van Donselaar, Antuma, Quakenbush & Warners EC-17-2281</i> (MICH, CALVIN)
<i>Solidago altissima</i> (not typically a bog species)		Dead-lake Bog	<i>Van Donselaar, Antuma, & Quakenbush EC-17-2879</i> (CALVIN)
<i>Xyris difformis</i>		Saul Lake Bog Dead-lake Bog	<i>Crow 10696</i> (CALVIN, MICH) <i>Antuma & Crow EC-17-2739</i> (CALVIN)

Miller’s Lake Bog

This small bog of only 3.68 hectares (9.1 acres) (Figure 4), including the open pond, was inventoried in 2015 and in 2018. Though small (17% the size of Saul Lake Bog and 10% the size of Dead-lake Bog), it was found to have a similar species richness (72), of which 97.2% are native species, and with only two species that are non-native (Table 1). A total of 21 species (29%) from this site have a *C* value of 8–10, nine of them showing an extremely high fidelity to undisturbed habitats with a *C* value of 10 (Table 2). The Mean *C* for the site is 5.8, the Native FQI is 50.2, and the Total FQI is a slightly diminished 49.2. Nearly as floristically rich as the other bogs, this is the third of our bogs studied with a Native FQI above the threshold value of 50 considered by Herman et al. (2001) to indicate a significant component of Michigan’s native biodiversity and natural landscapes.

As this bog is located within 0.5 mile of Emma Cole’s childhood home, a search was done to discover what plants she might have collected at this site in the 1890s. Extant herbarium records (MICHIGAN FLORA ONLINE 2011) and Cole’s (1901) *Flora* indicate the following species were observed or collected by

her from Miller's Lake: Swamp Beggar-ticks (*Bidens discoidea*), Grass-pink (*Calopogon tuberosus*), Sedge (*Carex oligosperma*), Spatulate-leaved Sundew (*Drosera intermedia*), Round-leaved Sundew (*D. rotundifolia*), Spikerush (*Eleocharis obtusa*), Rattlesnake Grass (*Glyceria canadensis*), Pinkweed (*Persicaria pensylvanica*), Green-fringed Orchid (*Platanthera lacera*), Rose Pogonia (*Pogonia ophioglossoides*), Beakrush (*Rhynchospora alba*), and Arrow-grass (*Scheuchzeria palustris*). Of these, *Calopogon tuberosus*, *Drosera intermedia*, *Platanthera lacera*, and *Persicaria pensylvanica* were not re-discovered in the bog during this study.

Comparison Between Historical and Present-day Bog Species

While our results identify certain changes in the bog flora of the Grand Rapids area over time, such differences are challenging to generalize. It is difficult to compare historical vs. contemporary inventories, even when dealing with a well-defined flora such as a bog flora, as a consequence of the nature of floristic surveys. Using Emma Cole's collection data proved to be challenging, as she was not often clear as to the exact collection site, or even specific habitat.

Historical Floristic Quality Assessment:

The historical catalog of bog species assembled from *Grand Rapids Flora* (Cole 1901) represents plants that might reasonably be expected to occur in any bog in the Grand Rapids area. Of the 142 species in the historical bog flora list, 47 (33%) bear a Coefficient of Conservatism (*C*) value between 8–10, and 26 show an extremely high fidelity to pristine conditions with a *C* value of 10. The historical bog flora (Table 1) has a very high Native FQI of 72.4 and a Total FQI of 71.5. There was only one non-native species—Woody Nightshade (*Solanum dulcamara*), common even in Cole's day, which occupied the swampy margins of bogs. Interestingly, *Solanum dulcamara* is one of the two or three non-native species in all three bogs examined in this study. While we might be faulted for having hand-selected the bog species from Cole's *Flora* for the historical list, thereby causing a remarkably high FQI, a similar result was obtained for the floristic list of Pennfield Bog in Calhoun County (Crow 1969b) with a total of 138 species (99.3% of them native). In that case, the Native FQI was similarly high, at 67.8, and the Total FQI was 67.3; a remarkable 40 of the species in that list were assigned a *C* value between 8 and 10, 15 of them with a *C* value of 10 (Crow, unpublished FQA data).

Tables 3 and 4 summarize the additions and apparent losses of species with strong affinities to the bog habitat between 1901 and 2018. A total of nine taxa observed in the current study have been added to the overall bog flora, six of which were new county records for Kent County, whereas eight species known to Emma Cole from the flora of the Grand Rapids area have not been documented since at least since 1939, and some not since the 1890s (MICHIGAN FLORA ONLINE 2011). Eight of the nine species added to the Grand Rapids area bog flora are native, while all of the species presumed lost are native. It is possible that some of those presumed lost may actually be a consequence of a lack of collecting and vouchering. *Salix pedicellaris* (a bog species) and *S. petiolaris* (a

TABLE 4. Taxa included in Cole’s *Flora of Grand Rapids*, believed now lost from the Grand Rapids area bog flora. Data for documenting specimens obtained from MICH database (MICHIGAN FLORA ONLINE 2011). Specimens by collector, date, locality, herbarium acronym; Kent County (K-Co.), Ottawa County (Ott-Co.).

Taxon	Documenting Specimens for Cole’s <i>Flora</i>	Most Recent Documenting Specimens
<i>Xyris torta</i>	<i>Cole</i> 1899, Little Bostwick Lake, Cannon Twp., K-Co. (MICH).	<i>Bazuin</i> 1939, Little Bostwick L., Cannon Twp., K-Co. (MSC); <i>Bazuin</i> 1940, Pond on E. Beltline n. of Knapp St., Grand Rapids Twp., K-Co. (MICH).
<i>Eriophorum gracile</i>	<i>Cole</i> 1897, Button Lake (now Emerald L.), Grand Rapids Twp., K-Co. (MICH); <i>Cole</i> 1899, Bronner Lake, Tallmadge Twp., Ott-Co. (MICH).	No specimens since 1899.
<i>Malaxis unifolia</i>	Cole’s <i>Flora</i> ; Saddle-bag Swamp, Grand Rapids Twp., K-Co.; no documenting specimens.	No records at MICH for K-Co. or Ott-Co.
<i>Platanthera blephariglottis</i>	<i>Cole</i> 1893, Vergennes Twp., K-Co. (MICH), Spruce L. 1893 (MICH); <i>Skeels & Shaddick</i> , 1893 Saddle-bag Swamp, Grand Rapids Twp., K-Co. (MSC); <i>Cole</i> 1898, Grand Rapids Twp., K-Co. (ALBC); <i>Daniels</i> 1899, Cassandra Bog, Alto, Bowne Twp. (MSC).	<i>Case</i> 1961, Aman Park, Tallmadge Twp., Ott-Co. (MICH); <i>Stoutamire</i> 1962, Aman Park, Tallmadge Twp., Ott-Co. (BHL).
<i>Platanthera ciliaris</i>	Cole’ <i>Flora</i> , Diamond Swamp, Burton Swamp; <i>Skeels & Shaddick</i> , 1893, Diamond Swamp, Grand Rapids Twp., K-Co. (MSC).	Cole (1901) considered this extirpated in Grand Rapids area by 1901.
<i>Platanthera flava</i>	<i>Shaddick</i> 1894, Diamond, Swamp, Grand Rapids Twp., K-Co. (MSC); <i>Mulliken</i> 1895, Burton Ave. [Swamp], Grand Rapids, K-Co. (MSC).	No specimens since 1895.
<i>Rhododendron groenlandicum</i>	Cole’s <i>Flora</i> , Burton Ave. Swamp, no specimen taken; Cole’s <i>Flora</i> , Saddle-bag swamp.	No documenting specimens.
<i>Salix pedicellaris</i>	<i>C. W. Fallas</i> 1893, sw of Grand Rapids, K-Co. (ALBC) <i>Cole</i> 1896, Webster Lake (Echo L.), Grand Rapids Twp., K-Co. (MICH)	<i>Bazuin</i> 1942, Pratt Lake, Lowell Twp., K-Co. (BHL); ca. 5 mi. east of Cole’s area.

more generalist wetland species) are both relatively common willows of southern Michigan and surely are overlooked species. *Salix pedicellaris* has not been documented for Kent County since 1942 (Table 4), and *S. petiolaris* (initially thought to be a “lost” species) had not been documented for the county since 1896—until David Warners picked up a staminate specimen in a fen on our first day of the 2019 field season (Hartwig, Crow, Warners EC-19-3750 CALVIN).

The non-native pest Glossy Buckthorn (*Frangula alnus*), which today is invasive in bogs, including two of our three bogs, as well as fens, cedar swamps, and other wet habitats, was not documented in Michigan until 1934, according to Voss and Reznicek (2012). Two other adventive species were encountered in our study and added to the West Michigan species pool (Table 5), but not regarded as additions to the Grand Rapids area bog flora (Table 3). One of these is clearly invasive in wetlands, Narrow-leaved Cattail (*Typha angustifolia*). Although this widespread species had been introduced in Michigan as early as 1877 (Voss and Reznicek 2012), it was apparently unknown to Emma Cole. Interestingly, we have found this species to be most invasive in wetlands that exhibit some disturbance, whereas we have not found this species to be aggressive in bogs, rather its occurrence in Saul Lake Bog was very sparse. The third adventive, the “dreaded” Purple Loosestrife (*Lythrum salicaria*), was unhappily discovered in Dead-lake Bog. As another invasive species that tends to be problematic in disturbed wetlands, thankfully only two plants were seen at this site.

Table 5 provides a comparison between the bog floras of our three contemporary study sites, the historic list generated from Cole (1901), and the species pool of bog plants generated for West Michigan. Our data indicate that a majority of bog species (83.9%) found in the Grand Rapids area by Emma Cole and her colleagues (142 species) were also found in the three bogs sampled in this study (122 species collectively) more than one century later, while only 16.2% were not found in the bogs sampled in this study.

Similarity Indices:

When comparing the collective present-day flora of our bogs to the historical list of bog species of Emma Cole, we calculated the Sørensen’s Index of Similarity because of its common use in botanical statistics. The Sørensen’s Index showed a similarity of 78.2% between the composite present-day floristic list of the bogs with the historical catalog of bog plants derived from Cole’s (1901) *Flora*. This indicates that the historical list of bog plants found in the Grand Rapids area has a very high degree of similarity to our present-day composite list. Table 6 compares the similarity of the bogs to each other, with similarity ranging from 55.4% to 59.6%, as well as to the historical bog list generated from the Emma Cole *Flora*, with a range of similarity from 57% to 63.3%. Acknowledging that, in general, plant communities represent a continuum of variability, two plant communities exhibiting a similarity greater than 50% can be regarded as the same community type (Curtis 1959; Bradley and Crow 2010). Since this threshold is well below that of the Sørensen’s indices for our comparisons, it is clear that the sites we inventoried all represent the same habitat type.

Application of the Simple Matching Index showed a strong similarity index

TABLE 5. Bog species in the species pool generated for West Michigan and their occurrence (indicated by “X”) in the list of plants of bogs generated from Cole’s (1901) *Flora* and the three sphagnum bogs inventoried during 2015–2018. Names of non-native species are in boldface.

Species Pool (166 Species)	Cole’s <i>Flora</i> (142 (Species)	Dead-lake Bog (76 Species)	Saul Lake Bog (75 Species)	Miller’s Lake Bog (72 Species)
<i>Acer rubrum</i> L.	X	X	X	X
<i>Acer saccharinum</i> Marshall			X	X
<i>Alisma subcordatum</i> Raf.	X			
<i>Alisma triviale</i> Pursh	X	X		
<i>Alnus incana</i> (L.) Moench	X		X	
<i>Andromeda glaucophylla</i> Link	X	X	X	X
<i>Arethusa bulbosa</i> L.	X			
<i>Aronia prunifolia</i> (Marshall) Rehder	X	X	X	X
<i>Asclepias incarnata</i> L.	X	X		
<i>Betula alleghaniensis</i> Britton	X	X	X	
<i>Betula pumila</i> L.	X		X	
<i>Bidens cernua</i> L.	X			
<i>Bidens connata</i> (Muhl.)	X			
<i>Bidens trichosperma</i> (Michx.) Britton	X	X	X	X
<i>Boehmeria cylindrica</i> (L.) Sw.	X	X	X	
<i>Brasenia schreberi</i> J. F. Gmel.	X		X	
<i>Calamagrostis canadensis</i> (Michx.) P. Beauv.	X	X	X	
<i>Calla palustris</i> L.	X		X	
<i>Calopogon tuberosus</i> (L.) Britton, Sterns & Poggenb.	X		X	
<i>Carex atlantica</i> subsp. <i>capillacea</i> (L. H. Bailey) Reznicek		X	X	
<i>Carex brunnescens</i> (Pers.) Poir.	X	X	X	
<i>Carex canescens</i> L.	X	X		
<i>Carex comosa</i> Boott	X			X
<i>Carex crinita</i> Lam.	X		X	
<i>Carex echinata</i> Murray	X		X	
<i>Carex gracillima</i> Schwein.	X			
<i>Carex interior</i> L. H. Bailey	X			
<i>Carex lasiocarpa</i> Ehrh.	X	X	X	X
<i>Carex limosa</i> L.	X			
<i>Carex lupulina</i> Willd.		X		
<i>Carex oligosperma</i> Michx.	X	X		X
<i>Carex pauciflora</i> Lightf.	X			
<i>Carex tenuiflora</i> Wahlenb.	X			
<i>Carex trisperma</i> Dewey	X	X	X	X
<i>Carex utriculata</i> Boott	X			
<i>Cephalanthus occidentalis</i> L.	X	X	X	X
<i>Ceratophyllum echinatum</i> A. Gray				X
<i>Chamaedaphne calyculata</i> (L.) Moench	X	X	X	X
<i>Cicuta bulbifera</i> L.	X	X		X
<i>Cladium mariscoides</i> (Muhl.) Torr.	X	X	X	
<i>Comarum palustre</i> L.	X	X	X	X
<i>Cornus amomum</i> Mill.	X	X		
<i>Cornus sericea</i> L.	X			
<i>Cyperus bipartitus</i> Kunth	X			
<i>Cyperus diandrus</i> Steud.	X			
<i>Cypripedium acaule</i> Aiton	X	X		

(Continued on next page)

TABLE 5. (Continued).

Species Pool (166 Species)	Cole's <i>Flora</i> (142 Species)	Dead-lake Bog (76 Species)	Saul Lake Bog (75 Species)	Miller's Lake Bog (72 Species)
<i>Decodon verticillatus</i> (L.) Elliott	X	X		X
<i>Drosera intermedia</i> Hayne	X	X	X	
<i>Drosera rotundifolia</i> L.	X	X	X	X
<i>Dulichium arundinaceum</i> (L.) Britton	X	X	X	X
<i>Eleocharis compressa</i> Sull.				
<i>Eleocharis obtusa</i> (Willd.) Schult.	X			X
<i>Eleocharis palustris</i> (L.) Some. & Schult.	X			
<i>Epilobium coloratum</i> Biehler	X	X		
<i>Epilobium leptophyllum</i> Raf.	X	X		
<i>Equisetum fluviatile</i> L.	X		X	
<i>Eriocaulon aquaticum</i> (Hill) Druce	X		X	
<i>Eriophorum angustifolium</i> Honck.	X			
<i>Eriophorum gracile</i> W. D. J. Koch	X			
<i>Eriophorum tenellum</i> Nutt.			X	
<i>Eriophorum vaginatum</i> L.	X			
<i>Eriophorum virginicum</i> L.	X	X	X	X
<i>Eupatorium perfoliatum</i> L.	X	X		
<i>Euthamia graminifolia</i> (L.) Nutt.	X	X		
<i>Eutrochium maculatum</i> (L.) E. E. Lamont	X	X		
<i>Eutrochium purpureum</i> (L.) E. E. Lamont	X	X		
<i>Frangula alnus</i> Mill.		X		X
<i>Galium trifidum</i> L.	X			X
<i>Gaylussacia baccata</i> (Wangenh.) K. Koch	X			X
<i>Glyceria canadensis</i> (Michx.) Trin.	X	X	X	X
<i>Hypericum boreale</i> (Britton) E. P. Bicknell				
<i>Ilex mucronata</i> (L.) M. Powell, V. Savolainen & S. Andrews	X			X
<i>Ilex verticillata</i> (L.) A. Gray	X	X	X	X
<i>Impatiens capensis</i> Meerb.	X	X		X
<i>Iris virginica</i> L.	X		X	
<i>Isotria verticillata</i> (Willd). Raf.				
<i>Juncus canadensis</i> Laharpe	X	X	X	X
<i>Juncus effusus</i> L.	X		X	X
<i>Juncus pylaei</i> Laharpe	X		X	
<i>Larix laricina</i> (Du Roi) K. Koch	X	X	X	
<i>Leersia oryzoides</i> (L.) Sw.	X			
<i>Lemna minor</i> L.	X		X	X
<i>Lemna trisulca</i> L.	X			
<i>Lemna turionifera</i> Landolt				X
<i>Liparis loeselii</i> (L.) Rich.				
<i>Ludwigia palustris</i> (L.) Elliott				
<i>Lycopodiella inundata</i> (L.) Holub			X	
<i>Lycopus americanus</i> Muhl.				X
<i>Lycopus uniflorus</i> Michx.	X	X	X	X
<i>Lysimachia terrestris</i> (L.) Britton, Sterns & Poggenb.	X		X	X
<i>Lysimachia thyrsiflora</i> L.	X		X	
<i>Lythrum salicaria</i> L.		X		
<i>Malaxis unifolia</i> Michx.	X			
<i>Menyanthes trifoliata</i> L.	X		X	X

(Continued on next page)

TABLE 5. (Continued).

Species Pool (166 Species)	Cole's <i>Flora</i> (142 Species)	Dead-lake Bog (76 Species)	Saul Lake Bog (75 Species)	Miller's Lake Bog (72 Species)
<i>Nuphar advena</i> (Aiton) W. T. Aiton	X	X	X	X
<i>Nymphaea odorata</i> Aiton subsp. <i>odorata</i>	X	X	X	
<i>Nyssa sylvatica</i> Marshall	X		X	X
<i>Onoclea sensibilis</i> L.	X		X	X
<i>Osmunda regalis</i> L.	X	X	X	X
<i>Osmundastrum cinnamomeum</i> (L.) C. Presl	X	X	X	X
<i>Peltandra virginica</i> (L.) Schott & Endl.	X	X	X	
<i>Persicaria amphibia</i> (L.) Delabare	X			X
<i>Persicaria sagittata</i> (L.) H. Gross	X			
<i>Phalaris arundinacea</i> L.	X	X		X
<i>Picea mariana</i> (Mill.) Britton, Sterns & Poggenb.	X		X	
<i>Pinus strobus</i> L.	X		X	
<i>Platanthera blephariglottis</i> (Willd.) Lindl.	X			
<i>Platanthera ciliaris</i> (L.) Lindl.	X			
<i>Platanthera clavellata</i> (Michx.) Luer	X			X
<i>Platanthera flava</i> (L.) Lindl.	X			
<i>Platanthera lacera</i> (Michx.) G. Don	X	X		
<i>Pogonia ophioglossoides</i> (L.) Ker Gawl.	X	X	X	X
<i>Pontederia cordata</i> L.	X			
<i>Populus tremuloides</i> Michx.	X	X		
<i>Potamogeton berchtoldii</i> Fieber				
<i>Potamogeton gramineus</i> L.	X			
<i>Potamogeton oakesianus</i> J. W. Robbins			X	
<i>Proserpinaca palustris</i> L.				X
<i>Quercus palustris</i> Münchh.				
<i>Rhynchospora alba</i> (L.) Vahl	X	X	X	X
<i>Rhynchospora fusca</i> (L.) W. T. Aiton		X		
<i>Rhododendron groenlandicum</i> (Oeder) Kron & Judd	X			
<i>Ribes triste</i> Pall.	X			
<i>Rosa palustris</i> Marshall	X	X	X	X
<i>Rubus hispidus</i> L.	X	X		
<i>Rumex verticillatus</i> L.				X
<i>Sagittaria latifolia</i> Willd.	X			X
<i>Salix candida</i> Willd.	X			
<i>Salix discolor</i> Muhl.	X		X	
<i>Salix exigua</i> Nutt.	X	X		
<i>Salix pedicellaris</i> Pursh	X			
<i>Salix petiolaris</i> Sm.	X			
<i>Sarracenia purpurea</i> L.	X	X	X	X
<i>Scheuchzeria palustris</i> L.	X	X		X
<i>Schoenoplectus acutus</i> (Bigelow) Á. Löve & D. Löve	X	X		
<i>Scirpus cyperinus</i> (L.) Kunth	X		X	X
<i>Scirpus pendulus</i> Muhl.	X			
<i>Scutellaria galericulata</i> L.	X			
<i>Scutellaria lateriflora</i> L.	X			
<i>Sium suave</i> Walter	X			X
<i>Solanum dulcamara</i> L.	X	X	X	X
<i>Sparganium emersum</i> Rehm.	X			

(Continued on next page)

TABLE 5. (Continued).

Species Pool (166 Species)	Cole's <i>Flora</i> (142 Species)	Dead-lake Bog (76 Species)	Saul Lake Bog (75 Species)	Miller's Lake Bog (72 Species)
<i>Spiraea alba</i> Du Roi	X	X		X
<i>Spiraea tomentosa</i> L.	X	X	X	X
<i>Thelypteris palustris</i> Schott	X	X	X	X
<i>Torreyochloa pallida</i> (L.) G. L. Church	X	X		
<i>Toxicodendron vernix</i> (L.) Kuntze	X	X	X	X
<i>Triadenum fraseri</i> (Spach) Gleason	X		X	X
<i>Triadenum virginicum</i> (L.) Raf.	X	X		X
<i>Typha latifolia</i> L.	X	X	X	X
<i>Typha angustifolia</i> L.			X	
<i>Utricularia cornuta</i> Michx.	X	X	X	
<i>Utricularia geminiscapa</i> Benj.	X			X
<i>Utricularia gibba</i> L.	X		X	X
<i>Utricularia intermedia</i> Hayne	X	X	X	
<i>Utricularia minor</i> L.	X			
<i>Utricularia purpurea</i> Walter	X			
<i>Utricularia vulgaris</i> subsp. <i>macrorhiza</i> (J. Le Conte) R. T. Clausen	X		X	X
<i>Vaccinium corymbosum</i> L.	X	X	X	X
<i>Vaccinium macrocarpon</i> Aiton	X	X	X	X
<i>Vaccinium oxycoccos</i> L.	X	X	X	X
<i>Viola blanda</i> Willd.	X			
<i>Viola macloskeyi</i> F. E. Lloyd	X	X		X
<i>Woodwardia virginica</i> (L.) Smith	X	X	X	X
<i>Xyris difformis</i> Chapm.		X	X	
<i>Xyris torta</i> Sm.	X			

value of 79.3% between the combined present-day bog flora, represented by our three inventoried bogs, and that of the historic Grand Rapids area bog flora, generated from Cole (1901). The Simple Matching Index reported even higher similarity values among the three present-day bogs as compared with the Sørensen's Index: Dead-lake Bog and Saul Lake Bog, 72.03% similarity; Saul Lake Bog and Miller's Lake Bog, 73.1%; and Miller's Lake and Dead-lake Bog, 72.5%.

TABLE 6. Sørensen's Index of Similarity for three present-day bogs and the historical list of bog species derived from Cole's (1901) *Flora*. Values to the lower left of the diagonal represent percent similarity; values to the upper right of the diagonal represent the number of species in common between individual bogs.

	Dead-lake Bog	Saul Lake Bog	Miller's Lake Bog	Historical Bog List (Cole's <i>Flora</i>)
Dead-lake Bog	—	45	41	69
Saul Lake Bog	59.6%	—	43	68
Miller's Lake Bog	55.4%	58.5%	—	61
Historical Bog List	63.3%	62.7%	57%	—

CONCLUDING REMARKS

Bogs are among the most easily recognizable habitat types in the Great Lakes region. They occupy low areas, are consistently wet, have an assemblage of characteristic species, and share similar substrate and hydrology. Another apparent trait, as indicated by this study, is that over time they can be amazingly resilient, even when their surrounding landscapes become severely altered. Perhaps this should not come as a great surprise, given that bogs themselves are not easily disturbed. Since they are already at a low point in the landscape, they are difficult to drain. Their “quaking” substrate makes them challenging to visit. Besides large-scale filling or peat harvesting for horticultural purposes, the most pressing present-day threat to bogs is excess nutrient runoff from surrounding agricultural or suburban uplands. But many bogs are simply avoided and therefore, even today, can offer remarkable representations of remnant pre-settlement landscapes.

Although bog flora has a remarkable consistency over time, a somewhat contrasting finding from this study is that the Sørensen index calculations revealed a greater similarity between the combined present-day bog flora and Cole’s historic flora (nearly 80%) than there is among the three present-day bogs (around 60%). In fact, each present-day bog was approximately as similar to the other two bogs as they were individually to the historic Cole bog flora. The relative distinctness of the present-day bogs is particularly noteworthy given that species richness and native-to-non-native ratios were essentially identical across all three (even though they varied 10-fold in size). These comparisons underscore that while bog flora regionally may be predictable and consistent over time, each individual bog is its own unique community. This recognition brings to mind a playful, favorite quip of the late Professor Warren “Herb” Wagner of the University of Michigan: “There are more different plant communities in Michigan than there are different species.”

Much of the focus of our Emma Cole Grand Rapids Flora Project has been to compare the present-day botanical landscape with that of the late 1800s. When considering bogs, with some regrettable losses, our comparison of over 100 years yields remarkable similarities. When left alone, bogs are habitats that appear to be highly conservative over time, much more so, for example, than we found with individual woodlots (Stockdale et al. 2019). And yet, gaining a sense of how much turnover has occurred during the past 120 years is also valuable as we look to the future. The changes documented in this study will be helpful when comparing future changes that are certainly already playing out as land alteration continues and climate change advances. We can only hope that the bogs of West Michigan will still be present and of sufficient quality to continue to delight and amaze their intrepid visitors 120 years hence.

ACKNOWLEDGMENTS

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ADDITIONS TO THE VASCULAR FLORA, AND NOTES ON THE PHYTOGEOGRAPHY, OF LAKE COUNTY, MICHIGAN

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ABSTRACT

The vascular flora of interior northern Lower Michigan is poorly represented in herbaria, with several counties ranking among the most sparsely collected in the Upper Great Lakes region. We initiated collecting in one of these counties, Lake County, in 2013. At the time, we were aware of 658 collections from the county, representing 437 vascular plant species. From 2013 through 2018, we added 698 specimens, representing 631 species, 559 of which were previously undocumented. As of early 2019, a total of 1,006 species for the county are confirmed, placing Lake County among the best-collected counties in northern Lower Michigan. Among the most noteworthy collections were 12 state-listed (Endangered, Threatened, and Special Concern) species and 30 species at their statewide or Lower Peninsula range limits. Additional collecting in Lake County and surrounding counties is recommended to catalog regional diversity and to substantiate or amend species distributions.

KEYWORDS: Lake County, Michigan, vascular flora, plant species, new records, phytogeography, tension zone

INTRODUCTION

Nearly 2,900 vascular plant species¹ growing outside of cultivation have been collected from Michigan, including approximately 1,800 native species and 1,100 non-native species (MICHIGAN FLORA ONLINE 2011). Floristic richness in Michigan follows a well-documented latitudinal gradient, declining from approximately 1,300–1,700 species per county in the southernmost counties to 1,000 species or fewer in the most depauperate northern counties (MICHIGAN FLORA ONLINE 2011). Although this diversity gradient is broadly supported

¹ MICHIGAN FLORA ONLINE (2011) and its predecessors treat species as the basic taxonomic unit, with very few exceptions (e.g., instances in which both native and non-native subspecies or varieties are present, as is the case for *Phragmites australis* and *Veronica beccabunga*). In this paper, “species” refers to searchable taxa on MICHIGAN FLORA ONLINE, with the understanding that associated statistics may include one or more infraspecific taxa.

by specimen records, many counties are poorly collected due to a variety of biological and cultural factors, such as the absence or presumed absence of unusual or attractive habitats, low road density, or distance from botanically active academic institutions and biological field stations (Fritsch 1993; MICHIGAN FLORA ONLINE 2011). Several counties in interior northern Lower Michigan are among the most sparsely collected in the Upper Great Lakes region (MICHIGAN FLORA ONLINE 2011; Kartesz 2015). Additional collecting in these counties is necessary for the enumeration of regional plant richness, resolution of species range limits, and detection of changes in the abundance and distribution of plant species, particularly those expected to be impacted by climate change. This paper documents our collecting efforts in Lake County from 2013 through 2018.

Description of the Study Area

Lake County covers 1,490 km² (38.6 × 38.6 km), centered at approximately 43.995°N, 85.811°W in northern Lower Michigan (Figure 1). Baldwin, the county seat, is 105 km (65 mi) north of Grand Rapids and 48 km (30 mi) east of Lake Michigan. The county is sparsely populated, with fewer than 12,000 permanent residents clustered in a few population centers, especially Baldwin,

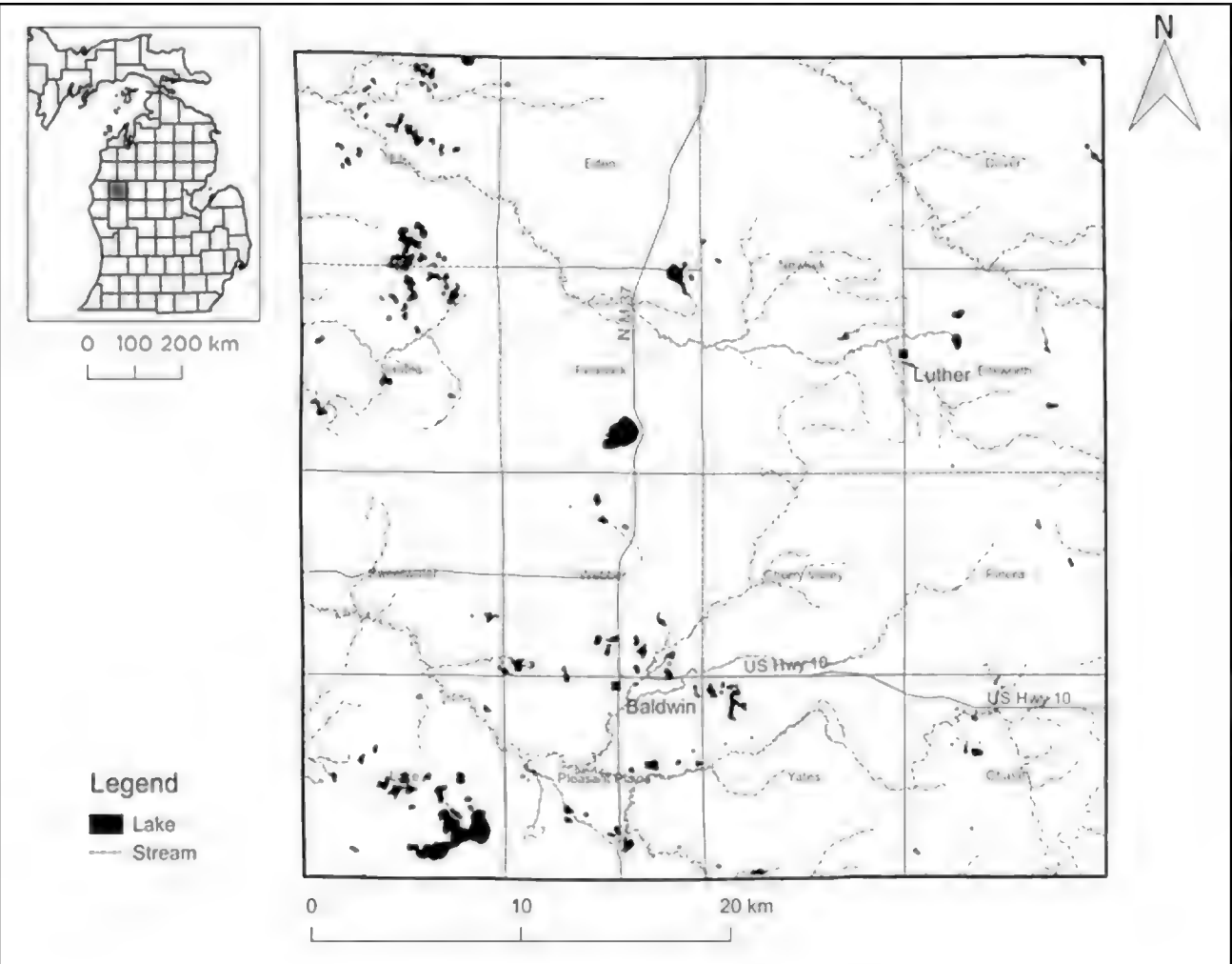


FIGURE 1. Location of Lake County in northern Lower Michigan, USA, and the location of the townships. (Basemap: State of Michigan–Michigan GIS Open Data.)

Idlewild, Chase, Luther, and the shores of several of the larger lakes (Lake County Planning Commission 2012; United States Census Bureau 2018). Approximately 7% of the land area is utilized for agriculture, much of it as forage-land, with limited areas of row crops (Lake County Planning Commission 2012; United States Department of Agriculture 2014). Forest cover exceeds 80%, much of it on state and federal land within the Pere Marquette State Forest and Manistee National Forest (Pugh et al. 2012).

Climate

Lake County has a warm-summer humid continental climate (i.e., Köppen–Geiger Classification *Dfb*), characterized by cold winters, warm summers, and no dry season (Kottek et al. 2006). Monthly average temperature (1981–2010 normals) at Baldwin ranges from -5.9°C (21.4°F) in January to 20.9°C (69.6°F) in July, with an annual average of 7.8°C (46.0°F), growing season (May–October) average of 16.0°C (60.8°F), and an average freeze-free period of 127 days (Arguez et al. 2010). Average liquid-equivalent annual precipitation at Baldwin is 87.9 cm (34.6 in) (Arguez et al. 2010). Average annual snowfall ranges from 183 cm (72 in) to 213 cm (84 in), with slightly lower amounts in the far southeastern part of the county and slightly higher amounts in the northern townships (Midwestern Regional Climate Center 2018a). Regional climate is trending warmer and wetter. Average annual temperature in the region has increased at a rate of $0.1^{\circ}\text{C}/\text{decade}$ ($0.2^{\circ}\text{F}/\text{decade}$) since 1895 and is projected to exceed 11°C (52°F) at Baldwin by 2100 (Girvetz et al. 2009; Midwestern Regional Climate Center 2018b). Average annual precipitation has increased at a rate of 1.6 cm/decade (0.6 in/decade) since 1895 and is projected to exceed 95 cm (37 in) at Baldwin by 2100 (Girvetz et al. 2009; Midwestern Regional Climate Center 2018b).

Landforms

Lake County is mantled by thick Wisconsin-aged glacial sediment overlying Mississippian (358.9–323.2 Ma) and Pennsylvanian (323.2–298.9 Ma) sandstone, shale, and limestone bedrock (Nicholson et al. 2004). The western townships consist of gently sloped outwash plains surrounding several hilly tracts associated with the Lake Border Moraine (Leverett and Taylor 1915) (Figure 2). Elevations range from approximately 200 m (650 ft) along the Pere Marquette River to 365 m (1,200 ft) on some of the moraine summits (United States Geological Survey 2017). The eastern townships comprise a portion of the Saginaw–Lake Michigan interlobate, a region marked by hummocky terrain on sandy glacial deposits exceeding 200 m (650 ft) in depth (Blewett et al. 2009; Schaetzl et al. 2013). Elevation generally exceeds 320 m (1,050 ft), with a high point of approximately 426 m (1,400 ft) in rural Pinora Township (United States Geological Survey 2017). These two primary physiographic regions are separated by a north and south trending escarpment traversing Newkirk, Cherry Valley, and Yates townships (Schaetzl et al. 2013).

Despite its namesake, fewer than 450 lakes or ponds of 0.04 ha (0.1 ac) or larger occur within Lake County, collectively covering less than 1% of its surface

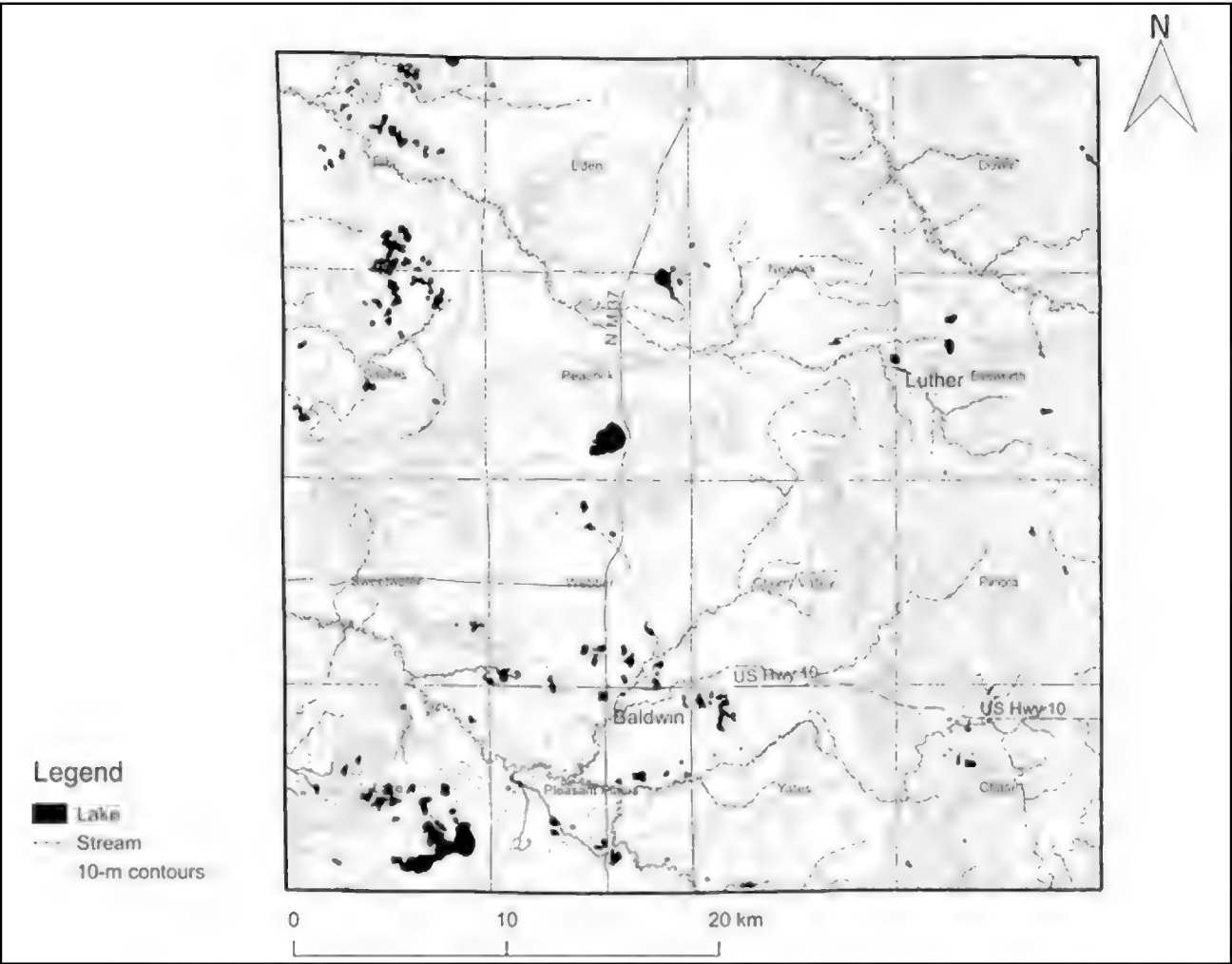


FIGURE 2. Topographic contour map of Lake County with 10-m contours. A prominent north and south trending escarpment (see arrow) separates the outwash plains and embedded hilly regions of western and central Lake County from the hummocky, high-elevation terrain of the eastern townships. (Basemap: State of Michigan–Michigan GIS Open Data; Topographic contours: U.S. Geological Survey–The National Map.)

area (Annable et al. 1991; Wolfson 2009). Only four of these lakes (Big Star, Wolf, Bass, and Syers) exceed 40 ha (100 ac) (Michigan Department of Natural Resources and Environment 2010). Lakes and drier kettles supporting wetland or upland vegetation are clustered in three areas: near Big Star Lake in the southwest; near Baldwin and Idlewild in Webber, Pleasant Plains, and Yates townships; and in the central portions of Elk and Sauble townships in the northwest.

Nine watersheds occur within the county (USDA, NRCS 2018). Major drainage networks are the Pine, Little Manistee, and Pere Marquette rivers and their tributaries. Lake County valley segments of all three rivers and their tributaries are characterized by cold water (mean July temperature <17.5°C/63.5°F), and all are designated trout streams, supporting noteworthy brown trout, rainbow trout, and Chinook salmon fisheries (Wang et al. 2012; O’Neal and Kolb 2015; Michigan Department of Natural Resources [MDNR], Institute for Fisheries Research 2017). Springs and headwater streams are frequent. Small portions of the northwestern and far eastern townships are drained by tributaries of the Big Sable and Muskegon rivers, respectively.

Soils

The two dominant soil orders in Lake County are Entisols and Spodosols (USDA, NRCS 1998). Entisols are poorly differentiated from parent sediments and lack diagnostic horizons (USDA, NRCS 2015). They are characteristic of young landscapes where soil development has taken place over a relatively short period of time, where the parent material is abrasion-resistant (e.g., silica), or where organic litter (e.g., pine needles) is absent or recalcitrant (Schaetzl 2009; USDA, NRCS 2015). In the Great Lakes region, these conditions occur on sand dunes and dry outwash plains (Schaetzl 2009). In Lake County, outwash plains are principally distinguished by Entisols such as Plainfield and Coloma sands (USDA, NRCS 2017) (see Figure 3 for a generalized map of surficial soil textures). These soils are droughty, nutrient-poor, and acidic and have negligible silt and clay content.

Like Entisols, Spodosols are characteristic of young landscapes and sandy parent materials, but they support distinctive horizons. Spodosols are the dominant soil order of northern Michigan, forming under mixed forest cover where seasonal water infiltration, often associated with a winter snowpack, leaches organic matter, aluminum, and iron from surface horizons to a distinctive subsurface known as a spodic horizon (Schaetzl 2009; USDA, NRCS 2015). In Lake

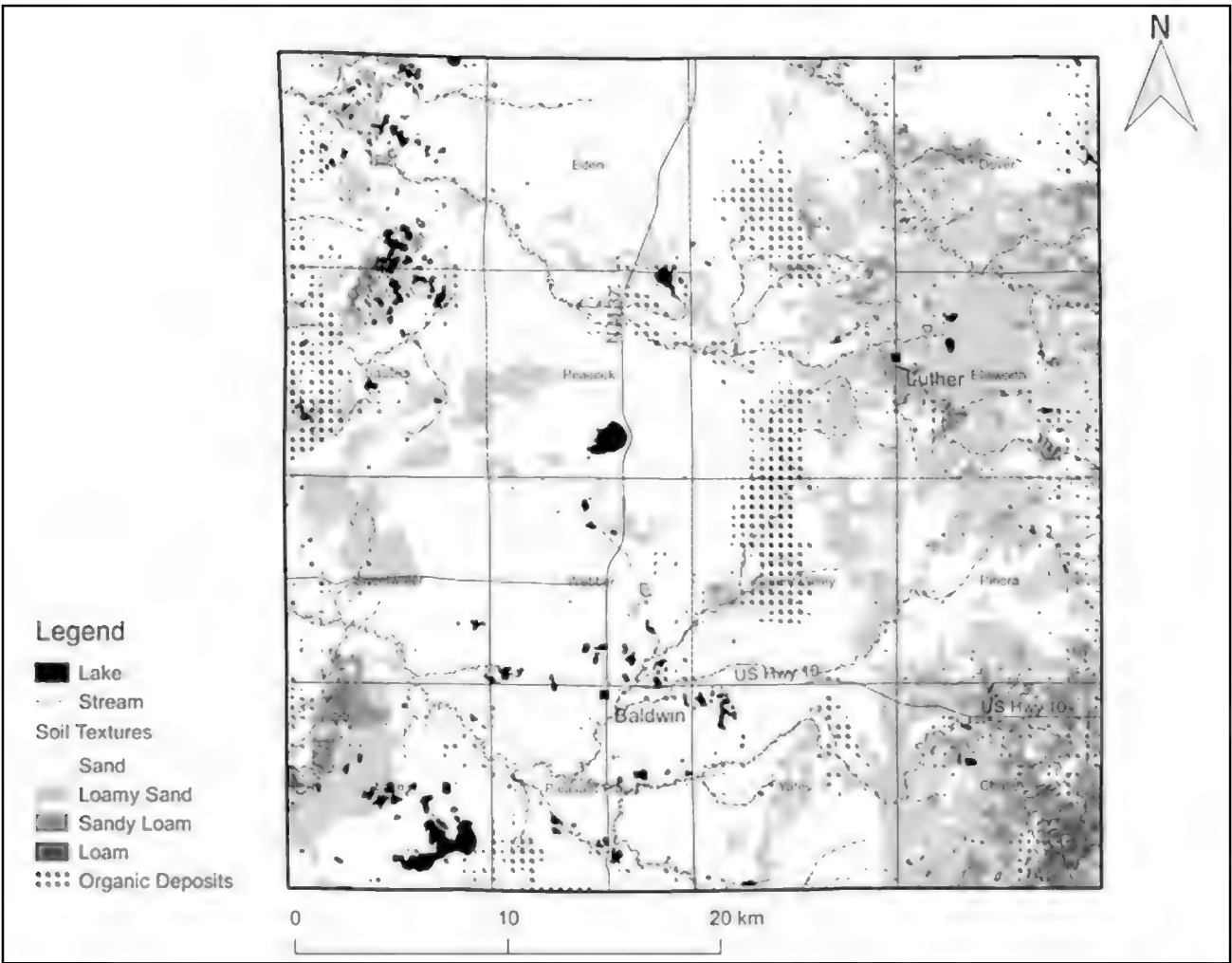


FIGURE 3. Generalized soil surface textures in Lake County. Note the preponderance of sandy textures and the restricted distribution of loamy textures. (Basemap: State of Michigan–Michigan GIS Open Data; Soil data: U. S. Department of Agriculture–Natural Resources Conservation Service.)

County, Spodosols are found on sandy moraines, where common map units include Montcalm-Graycalm complex, Grattan sand, and Rubicon sand (USDA, NRCS 2017). These soils share many physical characteristics with the Entisols, but some of the map units have higher clay and silt fractions and lower acidity (USDA, NRCS 2017).

Two minor soil orders comprise the remainder of Lake County soils: Alfisols and Histosols. Alfisols are characterized by the accumulation of clay in a sub-surface layer known as an argillic horizon (USDA, NRCS 2015). They tend to form on loamy glacial tills and under deciduous forest canopies and to have higher nutrient content and pH values relative to the sandier Entisols and Spodosols (Schaetzl 2009; USDA, NRCS 2015). Alfisols are the dominant soil order in southern Lower Michigan, but also occur sporadically in northern Michigan. In Lake County, Alfisols occur locally at the western and eastern margins of the county, with the largest area associated with a ground moraine east and south of Chase (USDA, NRCS 2015). Typical map units include Emmet-Montcalm complex, Kawkawlin loam, and Nester sandy loam (USDA, NRCS 2017).

Histosols are deep (>40 cm) accumulations of partially decayed organic matter, typically forming where soil saturation limits aerobic decomposition of plant materials (USDA, NRCS 2015). Histosols comprise approximately 12% of the land surface in Michigan (Schaetzl 2009). They are scattered throughout Lake County and occur in patches of up to several thousand hectares (e.g., in the Baldwin-Luther, Baylor, and Bear swamps). Typical soil units include Tawas-Roscommon association (shallow, circumneutral muck over sand), Lupton muck (deep, slightly alkaline muck), and Loxley peat (deep, acidic peat, as in bogs) (USDA, NRCS 2017).

Vegetation

The combination of poor soils and frequent fire historically favored the development of oak–pine forests and barrens on sandy outwash plains (Harvey 1920, 1922; Albert 1995; Albert and Comer 2008) (Figure 4). Sandy moraines supported similar communities, although topographic amelioration of the fire regime and other factors resulted in heavier forest cover. Loamier moraines supported white pine–mixed hardwood forest and, where fires were especially infrequent, beech–sugar maple–hemlock forest (Albert and Comer 2008). A variety of forested and non-forested wetlands occurred on wet mineral and organic soils throughout the county (Figure 5). Vegetation cover types mapped for the county by Comer et al. (1995) and their equivalent natural community types (Cohen et al. 2014) are listed in Table 1; generalized land cover circa 1800 is depicted in Figures 6 and 7.

Logging, fires, and land-clearing that took place during the timber boom of the late 1800s irrevocably altered the structure and, to a lesser degree, the composition of plant communities throughout Lake County (Harvey 1920, 1922; Albert 1995). Modern timber and wildlife habitat management, clearing and cultivation, drainage, development, fire suppression, and the introduction of pests, pathogens, and non-native species have all since impacted the majority of the vegetation in the county. Among the most significant changes to undeveloped



FIGURE 4. Oak–pine forests and openings (both natural and resulting from human activity) are emblematic of the sandy outwash plains in Lake County. Photo by A. K. Klain.



FIGURE 5. Rich conifer swamp dominated by *Thuja occidentalis* (northern white-cedar) along the Little Manistee River, Peacock Twp. Photo by A. K. Klain.

TABLE 1. Lake County circa 1800 vegetation types (Comer et al. 1995) and equivalent MNFI natural community types (Cohen et al. 2014) organized by characteristic physiographic settings. Some natural community types not listed here, such as dry sand prairie, occur or may occur in Lake County (Cohen et al. 2014) but were not mapped by Comer et al. (1995) due to their small size or other factors.

Landform/ <i>Soil</i>	circa 1800 Vegetation Type	Natural Community Type
Outwash Plain <i>Entisols</i> ; <i>Spodosols</i>	Jack Pine–Red Pine Forest	Dry Northern Forest
	White Pine–White Oak Forest White Pine–Red Pine Forest Mixed Pine–Oak Forest	Dry-mesic Northern Forest
	Pine Barrens	Pine Barrens
	Oak–Pine Barrens	Oak–Pine Barrens
End Moraine; Interlobate Moraine <i>Spodosols</i> ; <i>Alfisols</i>	Beech–Sugar Maple–Hemlock Forest Hemlock–White Pine Forest	Mesic Northern Forest
	White Pine–Mixed Hardwood Forest	Mesic Northern Forest Dry-mesic Northern Forest
	Mixed Pine–Oak Forest White Pine–White Oak Forest	Dry-mesic Northern Forest
Ground Moraine <i>Alfisols</i> ; <i>Spodosols</i>	Beech–Sugar Maple–Hemlock Forest	Mesic Northern Forest
	White Pine–Mixed Hardwood Forest	Mesic Northern Forest Dry-mesic Northern Forest
Depression <i>Histosols</i> ; <i>Alfisols</i> ; <i>Spodosols</i> ; <i>Entisols</i>	Cedar Swamp	Rich Conifer Swamp
	Mixed Conifer Swamp	Rich Conifer Swamp Hardwood–Conifer Swamp Poor Conifer Swamp Bog
	Mixed Hardwood Swamp Black Ash Swamp	Northern Hardwood Swamp
	Shrub Swamp/Emergent Marsh	Northern Shrub Thicket Northern Wet Meadow Emergent Marsh Submergent Marsh Intermittent Wetland

vegetation are altered forest canopy dominance patterns (e.g., from pine to oak and aspen or stump prairies on uplands and from northern white-cedar to red maple, tag alder, and cat-tail in wetlands), woody encroachment and reduction of herbaceous communities in remnant barrens, and degradation and reduction of shoreline wetlands due to water level manipulations and beaver activity (Albert 1995; Stearns 1997; Haxby et al. 2013a, 2013b).

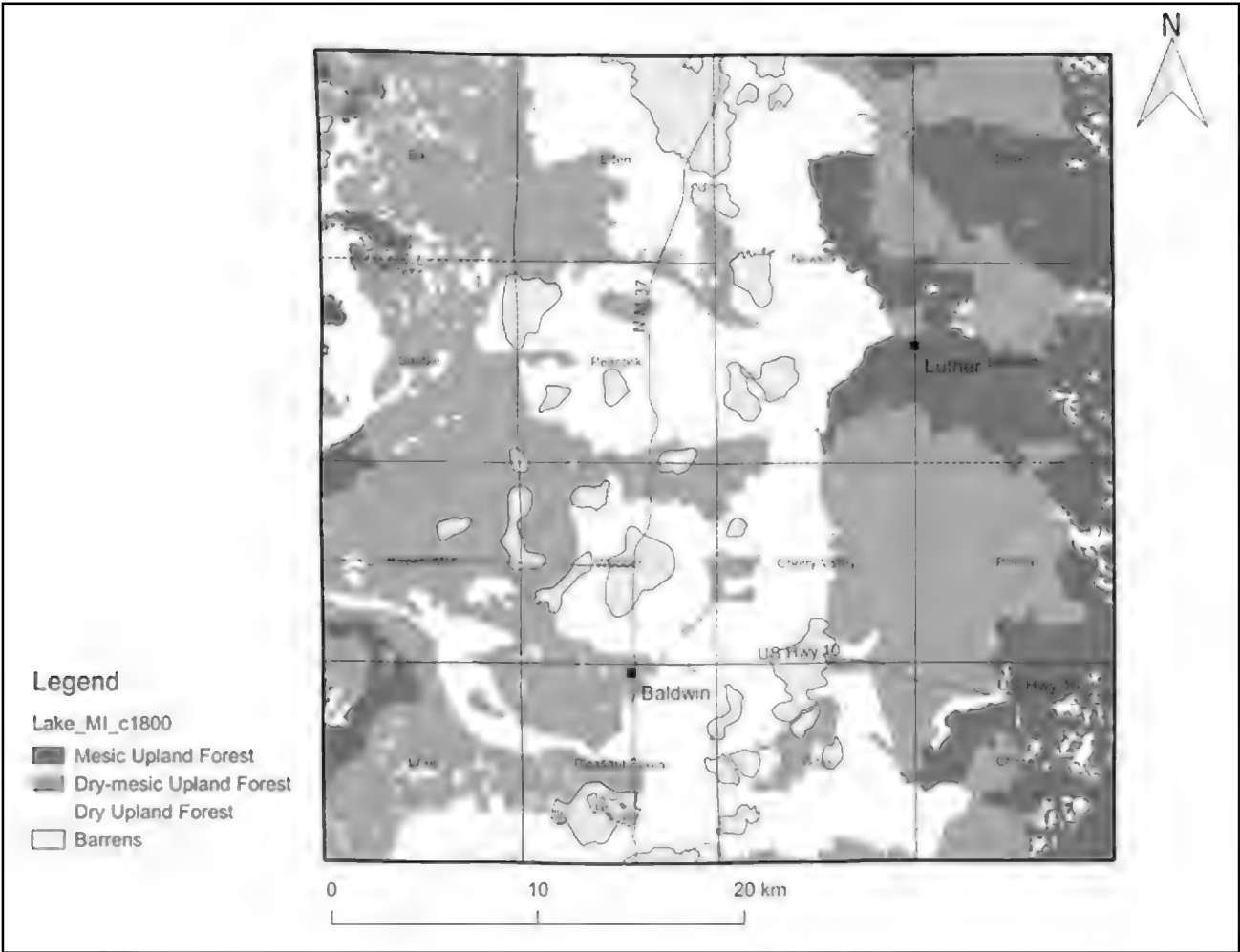


FIGURE 6. Circa 1800 upland vegetation, generalized from Comer et al. (1995). Dry and dry-mesic forests dominated by pines and oaks with embedded pockets of barrens characterized most of the county. Mesic forests were concentrated on finer-textured soils in the eastern townships. (Basemap and Data layer: State of Michigan–Michigan GIS Open Data.)

To date, Michigan Natural Features Inventory (MNFI) has identified 15 element occurrences, or high-quality examples, of natural communities within Lake County (MNFI 2018). Ten natural community types are represented, including four intermittent wetlands, three bogs, and one each of dry sand prairie, floodplain forest, northern hardwood swamp, oak–pine barrens, pine barrens, poor conifer swamp, rich conifer swamp, and wet-mesic sand prairie. Collectively, these 15 sites encompass approximately 595 ha (1,470 ac), or 0.3% of the county’s area (MNFI 2018). While Lake County has not been thoroughly inventoried by MNFI, these figures nevertheless indicate the extent and severity of human impacts to the vegetation and the resulting scarcity of sites resembling circa 1800 conditions.

Previous Floristic Work

The oldest known specimens from Lake County were collected between 1888 and 1891 by W. J. Beal, Professor of Botany at Michigan Agricultural College (MAC) (MICHIGAN FLORA ONLINE 2011) (one rare species probably collected by Beal is shown in Figure 8). Beal’s collections coincided with his work establishing and conducting research at the Baldwin Agricultural Experiment

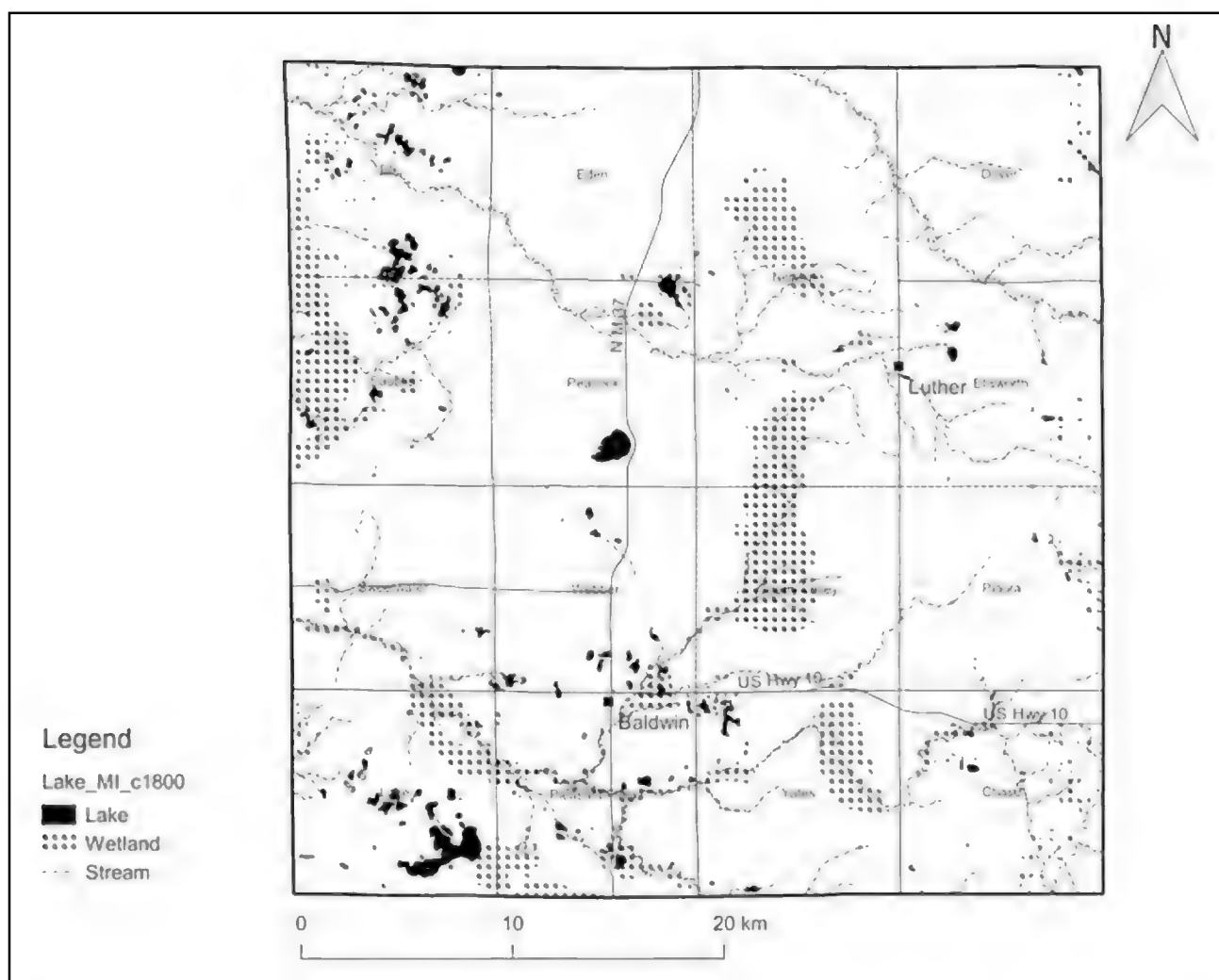


FIGURE 7. Circa 1800 wetland vegetation, generalized from Comer et al. (1995). Several large swamp forests occurred (and persist) in Lake County, especially at the base of the escarpment between Baldwin and Luther. Other wetland communities occurred mostly as small patches. (Basemap and Data layer: State of Michigan–Michigan GIS Open Data.)

Station, one of several small plots of land in northern Lower Michigan rented by MAC for the purposes of agricultural experimentation on jack pine plains (Michigan State Board of Agriculture 1888). After Beal ceded his role with the Experiment Stations in 1891, three decades passed with no new collections. From 1922 to 1938, 51 specimens were collected, many of these by the prominent botanist E. J. Palmer of the Arnold Arboretum at Harvard University (MICHIGAN FLORA ONLINE 2011).

Over half of the specimen records for Lake County date to the period from 1939 to 1976, coinciding with activity of its three most prolific collectors, C. W. Bazuin (130 specimens, 1939–1962), E. G. Voss (165 specimens, 1955–1973), and G. P. Stegmier (48 specimens, 1976) (MICHIGAN FLORA ONLINE 2011). Collecting slowed after 1976, with 38 specimens recorded from the period 1978–2007. In sum, a total of 658 collections, representing 437 vascular plant species, were mapped for Lake County at the initiation of our study (MICHIGAN FLORA ONLINE 2011). This total included 410 seed-bearing taxa mapped in *Field Manual of Michigan Flora* (Voss and Reznicek 2012), 14 taxa subsequently added to MICHIGAN FLORA ONLINE, and 13 ferns and other spore-bearing taxa not treated in the field manual or its predecessors (Voss 1972, 1985,



FIGURE 8. *Cirsium hillii* (Hill's thistle) was collected from the vicinity of Baldwin in July 1888, presumably by W. J. Beal. It remains locally frequent in the area. Newaygo Co., Michigan. Photo by B. S. Slaughter.

1996). Specimens collected just prior to the publication of Voss and Reznicek (2012) have since been added to MICHIGAN FLORA ONLINE (2011), increasing the total number of individually checked and confirmed² specimens collected prior to our work to 681 (MICHIGAN FLORA ONLINE 2011).

Early collections (1888–1930s) were made primarily from Baldwin and environs and consist nearly exclusively of terrestrial species. Collection of aquatic plants began in earnest in the late 1930s at Big Star Lake under the auspices of the Institute for Fisheries Research of the Michigan Department of Conservation (Voss 1972; MICHIGAN FLORA ONLINE 2011). Lake regions remained favored collecting locales through the 1970s. In addition to Big Star Lake, important stations included Bowman and Roby lakes in Lake Township; Cashion, Government, Hamlin, and Mench lakes near Baldwin; Syers and Little Syers lakes in Peacock and Eden townships; Totten Lake in Ellsworth Township; and Olga Lake

² From MICHIGAN FLORA ONLINE (2011): “On this site nothing is added to the flora or to any map without the supporting specimens having been individually checked and confirmed, both as to their identity and their status as wild plants collected in Michigan. We note this explicitly because the increased online availability of herbarium specimen label data . . . means that misidentifications that once slumbered anonymously in folders in herbaria are now enshrined in credible websites for all to see.”

in Dover Township. More recent collections were obtained from the Manistee National Forest and a few other scattered locations (MICHIGAN FLORA ONLINE 2011).

METHODS AND MATERIALS

Site Selection

Initial collections in 2013 were gathered from the authors' field project sites on the Manistee National Forest (HMNF) and private land enrolled in the Michigan Department of Natural Resources (MDNR) Landowner Incentive Program. Additional collection sites were identified through a combination of aerial photographic interpretation, field reconnaissance, drive-by inspections, site leads derived from MNFI (2018), herbarium records, and suggestions and field data from biologists and foresters with the Baldwin Field Office of MDNR and the Baldwin/White Cloud Ranger District of the Manistee National Forest. Lists of target species were generated from these leads and revised during and after each field season.

Collections

Voucher specimens were collected during the period from May 2013 to September 2018. GPS coordinates and notes on abundance, habitat, and associated species were recorded for most collections. Determinations were made by the authors, and specimens were examined and redetermined, where necessary, by A. A. Reznicek at the University of Michigan Herbarium (MICH). All specimens were mounted, databased, and deposited at MICH. Specimen data are searchable on MICHIGAN FLORA ONLINE (2011), coincident with periodic updates of the maps and specimen records.

RESULTS

A total of 698 specimens were collected, representing 631 species. Among these were 559 species newly vouchered³ from Lake County, including 409 native species and 150 non-native species (MICHIGAN FLORA ONLINE 2011) (Table 2; Appendix 1). Twelve species listed as Endangered, Threatened, or Special Concern in Michigan (MNFI 2009) were collected, including eight species not previously collected from Lake County, two species previously collected from other locations within the county, and two species that had been reported but not substantiated with collections (MICHIGAN FLORA ONLINE 2011; MNFI 2018) (Table 3; Appendix 1).

Specimens were collected from 14 of the 15 townships in the county (Figure 9). Among the 698 specimens, 512 (73%) were collected from southern Lake County, and 186 (27%) were collected from northern Lake County. Important collecting locales included the floodplains of the Pere Marquette (Pleasant Plains, Lake, and Sweetwater townships) and Pine (Dover and Newkirk townships) rivers; the Village of Baldwin (Pleasant Plains and Webber townships); Baldwin-Luther Swamp and vicinity (Cherry Valley Township); "Idlewild Bar-

³ This figure includes only those specimens individually checked and confirmed for inclusion on MICHIGAN FLORA ONLINE. Unverified specimens from Lake County exist in several herbaria and are searchable on the Consortium of Midwest Herbaria (2019) website. Some of these may represent taxa we list here as "newly vouchered," but they are omitted here in concordance with the website's policy quoted above in footnote 2.

TABLE 2. Taxonomic summary of species newly vouchered for Lake County. Native Species include those native to Michigan, but not necessarily to Lake County (e.g., *Gleditsia triacanthos*).

Group	Families	Genera	Native Species	Adventive Species	Total Species
Pteridophytes	6	16	23	0	23
Gymnosperms	2	4	4	2	6
Monocots	17	73	159	31	190
Dicots	73	208	223	117	340
TOTALS	98	301	409	150	559

rens” (Yates Township); and Elbow Lake and Duck Marsh in Elk Township (Figure 9). Eden, Ellsworth, and Sauble townships received the least attention, with one collection from each.

DISCUSSION

Status of the Flora

Prior to our work, only 437 vascular plant species were vouchered from Lake County, ranking 78th among the 83 Michigan counties. With the addition of our recent collections and several independent collections from the same period, a total of 1,006 species have now been vouchered from Lake County, which now ranks 28th (Table 4) (MICHIGAN FLORA ONLINE 2011). This includes 807 native species (28th) and 199 non-native species (30th). Among the 30 counties in

TABLE 3. State-listed species vouchered from Lake County*. E = Endangered; T = Threatened; SC = Special Concern. First collection dates based on specimens examined for MICHIGAN FLORA ONLINE (2011).

Species	Common Name	State Status	First Collection
<i>Asclepias ovalifolia</i>	dwarf milkweed	E	2016
<i>Berula erecta</i>	water-parsnip	T	2017
<i>Cirsium hillii</i>	Hill’s thistle	SC	1888
<i>Eleocharis engelmannii</i>	Engelmann’s spike-rush	SC	2014
<i>Eleocharis melanocarpa</i>	black-fruited spike-rush	SC	1995
<i>Geum triflorum</i>	prairie-smoke	T	2007
<i>Helianthus hirsutus</i>	hairy sunflower	SC	2017
<i>Lipocarpa micrantha</i>	dwarf-bulrush	SC	1946
<i>Poa paludigena</i>	bog bluegrass	T	1890
<i>Prunus umbellata</i>	Alleghany plum	SC	1925
<i>Pycnanthemum verticillatum</i>	Whorled mountain mint	SC	2018
<i>Rhynchospora macrostachya</i>	tall beak-rush	SC	2014
<i>Scleria pauciflora</i>	few-flowered nut-rush	E	2014
<i>Scleria triglomerata</i>	tall nut-rush	SC	2014
<i>Sisyrinchium strictum</i>	blue-eyed-grass	SC	2014
<i>Wolffia brasiliensis</i>	pointed water meal	T	2012

**Brickellia eupatorioides* (false boneset, SC) was recently collected from a grassland planting where it was presumably introduced. *Boechera missouriensis* (Missouri rock cress, SC) is reported by Michigan Natural Features Inventory (MNFI 2018) but not substantiated with specimens.

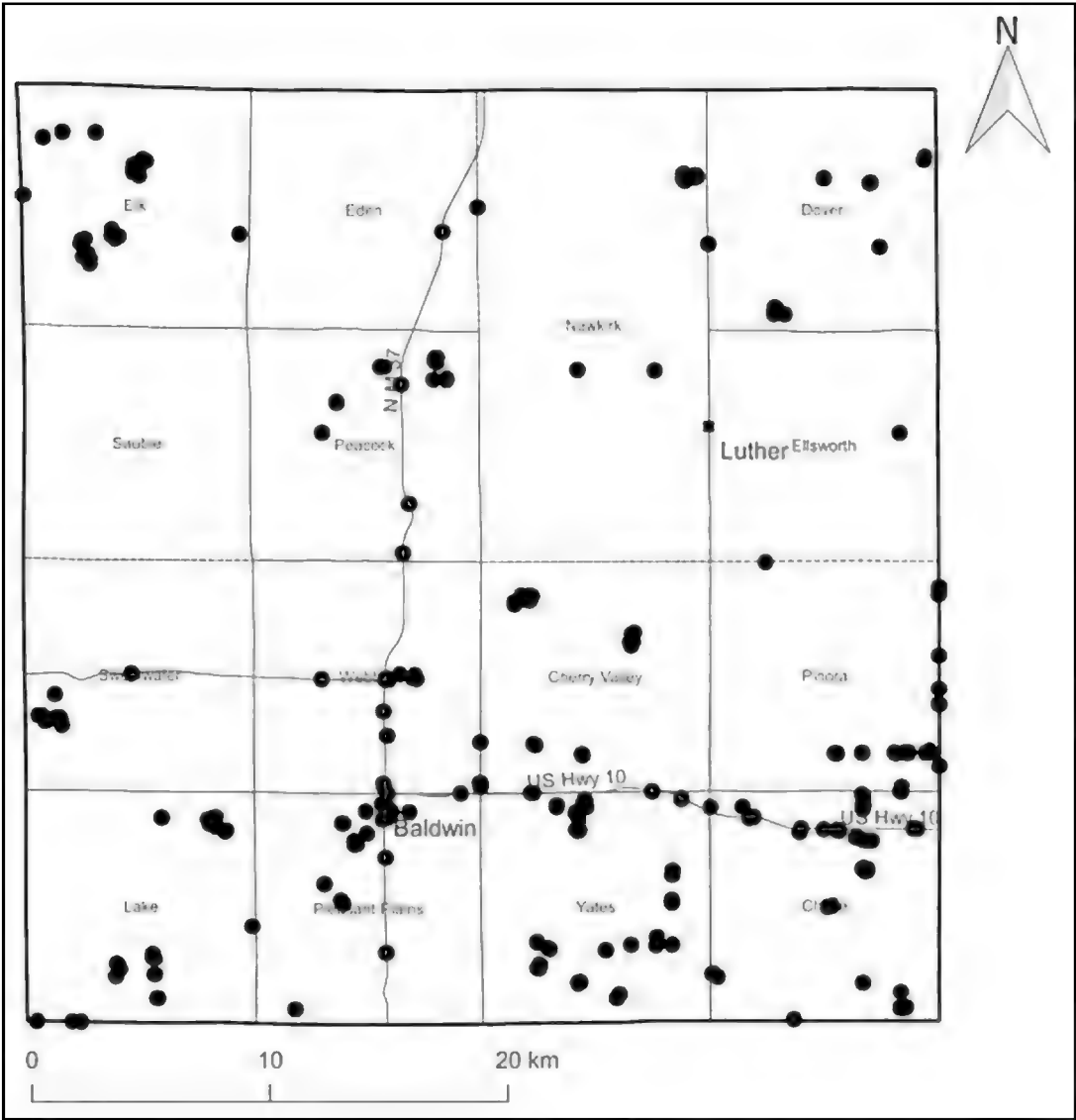


FIGURE 9. Collection locations of all 698 collections made in this study. (Basemap: State of Michigan–Michigan GIS Open Data.)

northern Lower Michigan, Lake County ranks sixth (fifth for native species). Based on our observations, HMNF stand data (P. R. McGahn, pers. comm.), and species present in adjacent counties but not yet documented from Lake County, actual vascular plant richness likely exceeds 1,200 species.

We collected more specimens in 2013–2018 than had been collected over the preceding 125 years, increasing the total number of confirmed records for Lake

TABLE 4. Collection statistics for Lake County, derived from MICHIGAN FLORA ONLINE (2011), as of January 2019. Rank: Rank for each category among counties (1 = highest, 83 = lowest). Range: Lowest value (County)–highest value (County).

Category	Number	Rank	Range
Vouchered Species	1006	28	346 (Gladwin)–1750 (Washtenaw)
Vouchered Native Species	807	28	278 (Gladwin)–1207 (Kalamazoo)
% of Total Flora, Native Species	80.2%	45	67.9 (Wayne)–88.8 (Wexford)
Vouchered Non-native Species	199	30	41 (Osceola)–558 (Washtenaw)
% of Total Flora, Non-native Species	19.8%	39	11.2 (Wexford)–32.1 (Wayne)
Total Collections	1381	51	410 (Gladwin)–13878 (Washtenaw)
Avg. No. Collections per Species	1.4	79	1.2 (Gladwin)–9.8 (Keweenaw)

County to 1,381 and improving its standing among Michigan counties from 79th to 51st (Table 4). Because we targeted new county records, most species are represented by only one collection, which is reflected in the low ratio of 1.4 specimens per species (Table 4). This ratio is below 2.0 for only three other counties with 1,000 or more confirmed species, all of which have been the focus of targeted collecting in recent decades (Fritsch 1993; MICHIGAN FLORA ONLINE 2011; W. S. Martinus and R. G. Schipper, pers. comm.). Additional collecting of species substantiated by only one specimen is recommended to support a more thorough treatment of the Lake County flora in its entirety.

Rare Species

Sixteen naturally occurring state-listed (Endangered, Threatened, and Special Concern) species have now been collected from Lake County (Table 3). Most of these occur in two natural communities—intermittent wetland (seven species) and oak–pine barrens (five species) (Table 3; see also the *Species at the Edge of Their Range* section below). The remainder occur in cold seeps (two species), beaver ponds (one species), and old fields (one species). Three additional listed species have been reported but are omitted from Table 3. *Boechnera missouriensis* (Missouri rock-cress, SC) is reported from two localities by MNFI (2018) but is not substantiated with specimens. *Brickellia eupatorioides* (false boneset, SC) was collected from a grassland planting where it was likely introduced. *Artemisia ludoviciana* (western mugwort, ST) is presumed to be native along the Menominee River in Menominee County but occurs in Lake County (and elsewhere in Michigan) as an introduction (MICHIGAN FLORA ONLINE 2011).

Statewide, rare species richness tends to decline with increasing latitude and distance from the Great Lakes shoreline⁴ (Figure 10). The southernmost counties are particularly rich in rare species due to proximity to the state line (and hence the presence of edge-of-range taxa that barely enter the state), presence of uncommon habitats, and the scarcity of relatively undisturbed remnants of historically common habitats. Berrien County in the southwestern corner of the state has the richest assemblage of rare species (119), which comprise 10% of its native flora (MICHIGAN FLORA ONLINE 2011). Most counties in interior northern Lower Michigan, in comparison, support fewer than 10 vouchered rare taxa (Figure 10). The somewhat higher figure in Lake County is due to the presence of intermittent wetlands, which otherwise occur primarily to its southwest (see the *Species at the Edge of Their Range* section below). Among neighboring counties, Newaygo County shares 12 (75%) of the 16 rare species found in Lake County, followed by Mason County, with eight (50%), and Oceana County, with four (25%). This is unsurprising, as contiguous portions of these counties share similar landforms, soils, and vegetation (Albert 1995; Schaetzl et al. 2013; United States Environmental Protection Agency 2013) (Figure 10).

⁴ In the Upper Peninsula, rare species richness is higher than in northern Lower Michigan due to the presence of an assortment of primarily western, boreal, and arctic-alpine species, especially on Isle Royale (Keweenaw County). Of the 127 species known in Michigan only from the Upper Peninsula, 108 (83%) are state-listed (MNFI 2009; MICHIGAN FLORA ONLINE 2011).

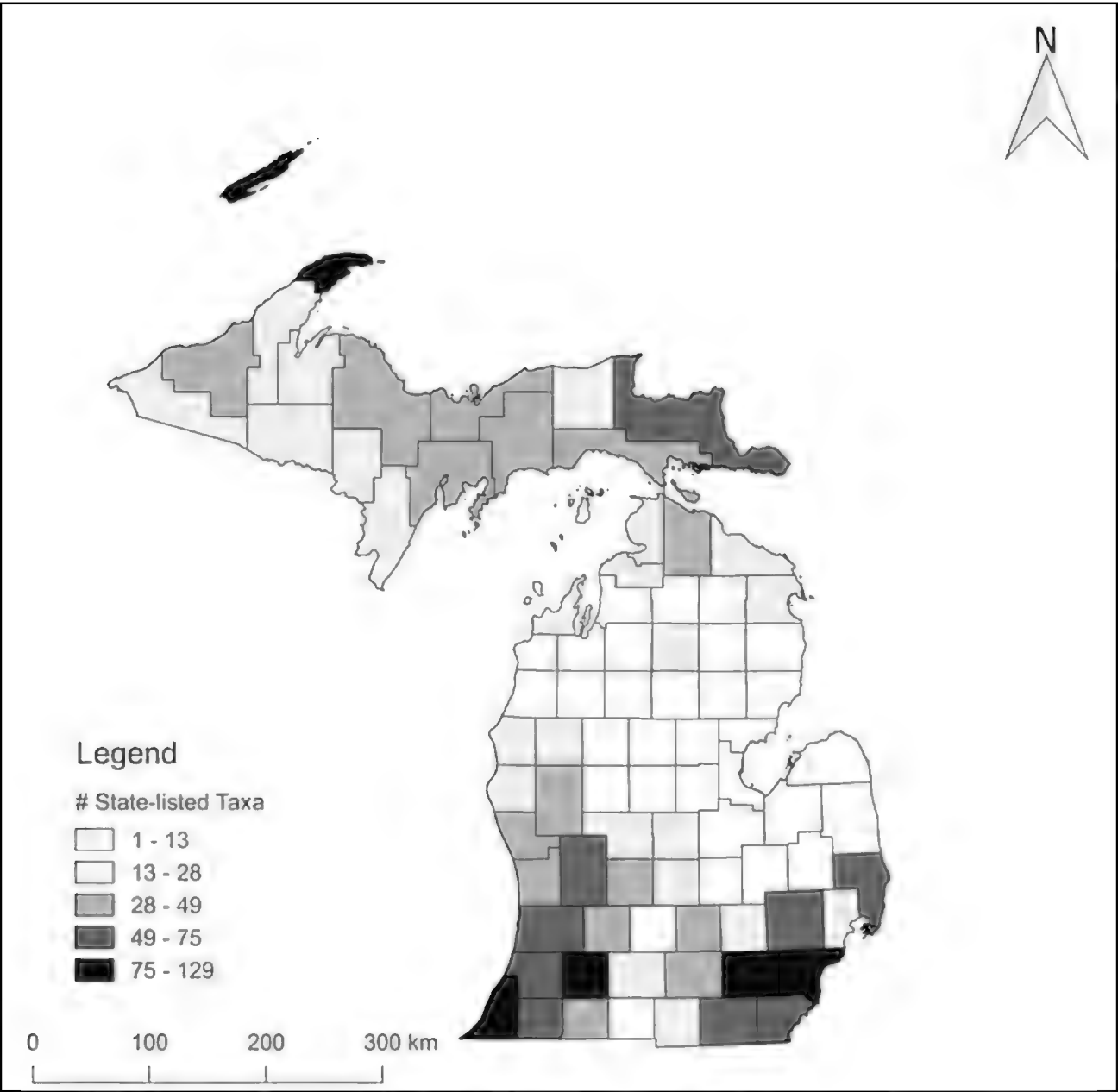


FIGURE 10. The number of vouchered, naturally occurring state-listed species (endangered, threatened, special concern) per Michigan county, derived from MNFI (2009) and MICHIGAN FLORA ONLINE (2011). (Basemap: State of Michigan–Michigan GIS Open Data.)

Species at the Edge of Their Range

The presence of a vegetation tension zone extending approximately east to west across the center of Michigan’s Lower Peninsula was documented by the beginning of the 20th Century (McCann 1979; Andersen 2005). The tension zone marks a relatively abrupt transition in the dominant vegetation from the hardwood-dominated forests of southern Lower Michigan to the mixed hardwood-conifer forests emblematic of northern Lower Michigan, corresponding to gradients in regional climate, physiography, soils, and hydrology (Albert 1995). The tension zone is typically mapped as extending from Muskegon County northeastward to Bay County and continuing northeastward across Saginaw Bay and the Thumb or angling southeast to Port Huron (McCann 1979; Andersen 2005). Lake County is approximately 40 to 80 km north of the transition zone, and its

dominant plant communities (e.g., dry northern forest, dry-mesic northern forest) are typical of northern Michigan (Cohen et al. 2014).

In addition to dividing broad vegetation zones, the tension zone corresponds with the northern range limits of a number of southern plant species. Range limits of northern plants, on the other hand, are not concentrated in the same region (McCann 1979). Our findings reflect this pattern. Among the species newly vouchered from Lake County, 27 are at their northern (latitudinal) range limits within the state and only three are at their southern statewide range limits. The county flora in its entirety includes 35 native species at their northern statewide or Lower Peninsula range limits and only six species at their southern range limits (MICHIGAN FLORA ONLINE 2011) (Tables 5–7).

Species at their northern range limits in Lake County cluster in four principal habitats. Eight of the species were collected from shallow, seasonally and inter-annually desiccated kettle depressions known as intermittent wetlands (Tables 5, 6). Several of these species are disjunct from, or have ranges centered on, the Atlantic and Gulf coastal plains and occur in Michigan primarily in the southwestern counties, where their presence typifies a variant of intermittent wetland known as coastal plain marsh (Reznicek 1994; Kost and Penskar 2000; Cohen and Kost 2007; Cohen et al. 2014). A notable assemblage of these species occurs at and near Duck Marsh in Elk Township and is discussed further by Slaughter

TABLE 5. Species at their northernmost statewide range limits in Lake County and the natural communities associated with each, indicated by “x”. Natural community classification follows Cohen et al. (2014). BAR = oak–pine or pine barrens; BOG = bog or poor conifer swamp; CS = rich conifer swamp or hardwood–conifer swamp; DMF = dry-mesic northern forest; FF = floodplain forest; IW = intermittent wetland; MF = mesic northern forest; OTH = other.

Species	BAR	BOG	CS	DMF	FF	IW	MF	OTH
<i>Agrimonia pubescens</i>				x				
<i>Aristida purpurascens</i>						x		
<i>Bidens discoidea</i>			x					
<i>Carex laxiculmis</i> var. <i>copulata</i>					x			
<i>Cornus florida</i>				x				
<i>Crataegus calpodendron</i>					x			
<i>Desmodium illinoense</i>	x							
<i>Desmodium rotundifolium</i>	x			x				
<i>Dichanthelium commutatum</i> subsp. <i>ashei</i>				x				
<i>Dichanthelium dichotomum</i>				x				
<i>Eleocharis engelmannii</i>						x		
<i>Eleocharis melanocarpa</i>						x		
<i>Enemion biternatum</i>							x	
<i>Lespedeza violacea</i>	x			x				
<i>Muhlenbergia schreberi</i>				x				
<i>Pycnanthemum verticillatum</i>						x		
<i>Rhynchospora macrostachya</i>						x		
<i>Rotala ramosior</i>						x		
<i>Samolus parviflorus</i>					x			
<i>Scleria pauciflora</i>						x		
<i>Scleria triglomerata</i>						x		
<i>Wolffia brasiliensis</i>		x						x

TABLE 6. Species at their northernmost Lower Peninsula range limits in Lake County and the natural communities associated with each, indicated by “x”. Natural community classification follows Cohen et al. (2014). BAR = oak–pine or pine barrens; BOG = bog or poor conifer swamp; CS = rich conifer swamp or hardwood–conifer swamp; DMF = dry-mesic northern forest; FF = floodplain forest; IW = intermittent wetland; MF = mesic northern forest; OTH = other.

Species	BAR	BOG	CS	DMF	FF	IW	MF	OTH
<i>Acalypha rhomboidea</i>							x	x
<i>Allium canadense</i>					x			
<i>Cyperus strigosus</i>					x			
<i>Dichanthelium clandestinum</i>					x			
<i>Dichanthelium praecocius</i>								x
<i>Geum triflorum</i>	x							
<i>Helianthus hirsutus</i>								x
<i>Leersia virginica</i>					x			
<i>Micranthes pensylvanica</i>			x					
<i>Muhlenbergia frondosa</i>					x			x
<i>Podophyllum peltatum</i>							x	
<i>Ranunculus fascicularis</i>	x							
<i>Symphyotrichum oolentangiense</i>	x			x				

TABLE 7. Species at their southernmost statewide range limits in Lake County and the natural communities associated with each, indicated by “x”. Natural community classification follows Cohen et al. (2014). BAR = oak–pine or pine barrens; BOG = bog or poor conifer swamp; CS = rich conifer swamp or hardwood–conifer swamp; DMF = dry-mesic northern forest; FF = floodplain forest; IW = intermittent wetland; MF = mesic northern forest; OTH = other.

Species	BAR	BOG	CS	DMF	FF	IW	MF	OTH
<i>Arceuthobium pusillum</i>		x						
<i>Asclepias ovalifolia</i>	x							
<i>Carex adusta</i>								x
<i>Oxalis acetosella</i>			x					
<i>Sibbaldiopsis tridentata</i>	x							
<i>Sorbus americana</i>								x

(2016) (an example of these species is shown in Figure 11). A larger cluster of intermittent wetlands in the vicinity of Big Star Lake in Lake Township merits additional exploration.

Riparian forests were lucrative collecting grounds, supporting both northern and southern floristic elements. Among the latter are eight species at their northern range limits, all collected from the wooded floodplain of the Pere Marquette River (Tables 5, 6). The extra-latitudinal presence of “southern” plant species in riparian habitats is well-documented and is thought to be related to microclimatic amelioration (Tepley et al. 2004; MICHIGAN FLORA ONLINE 2011). However, empirical evidence for the presence of distinct riparian microclimates in eastern North America is scarce (Brooks and Kyker-Snowman 2009), and other variables such as soil characteristics and post-glacial dispersal may be responsible for the presence of these range-limited species. In general, species richness within Michigan floodplain forests declines from south to north (Tepley



FIGURE 11. *Rhynchospora macrostachya* (tall beak-rush), which is state-listed as a Special Concern species, is a locally frequent sedge of intermittent wetlands occurring at its northern statewide range limit in northwestern Lake County and northeastern Mason County. Photo by B. S. Slaughter, Van Buren Co., Michigan.

et al. 2004) but attempts to make inferences at finer scales are hampered by an absence of data.

Among upland habitats, species at their northern range limits occurred primarily in dry-mesic northern forest and oak–pine barrens. Noteworthy are several legumes, including *Desmodium illinoense* (prairie tick-trefoil), *D. rotundifolium* (round-leaved tick-trefoil), and *Lespedeza violacea* (bush-clover). These and several other species prevalent in southern Michigan prairies and savannas, such as *Lespedeza hirta* (hairy bush-clover), *Lupinus perennis* (wild lupine), and *Ranunculus fascicularis* (early buttercup), occur locally within Lake County (mostly in the southern townships) but are conspicuously absent from the jack pine plains of north-central and northeastern Lower Michigan⁵, perhaps due to inhospitable climate, dispersal limitations, soil characteristics, absence of nitrogen-fixing symbionts, or other factors (Bordeleau and Prévost 1994; Comer 1996; Chapman and Brewer 2008; MICHIGAN FLORA ONLINE 2011; Simonson et al. 2017).

Although only three species at their northern range limits were collected from mesic northern forest (Table 6), several species known to occur north of Lake

⁵ Of the jack pine plains flora of northern Lower Michigan, W. J. Beal remarked that the absence of Fabaceae was “most remarkable of all” (Michigan State Board of Agriculture 1888).



FIGURE 12. The showy biennial *Hydrophyllum appendiculatum* (great waterleaf) occurs very locally in rich forests in the southeastern part of the county. Photo by B. S. Slaughter, Cass Co., Michigan.

County only in lakeshore counties or along rivers were collected, including *Hydrophyllum appendiculatum* (great waterleaf), *H. canadense* (Canada waterleaf) (Figure 12), *Persicaria virginiana* (jumpseed), and *Symphotrichum cordifolium* (heart-leaved aster) (MICHIGAN FLORA ONLINE 2011). These species were concentrated in Chase Township in the southeastern corner of the county, where a lobe of nutrient-rich, loamy glacial till supports a few relatively intact woodlots dominated by *Acer saccharum* (sugar maple), *Fagus grandifolia* (American beech), and *Tilia americana* (basswood). Such forests occur with greater prevalence just east and north of Lake County (Burger and Kotar 2003; USDA, NRCS 2015). Because they are agriculturally productive, these lands are primarily in private ownership and are relatively inaccessible to botanists. Exploration of mesic woodlots in northwestern Lower Michigan is essential for the demarcation of range limits of many principally southern forest herbs.

Species at their southern statewide range limits are few and apparently localized (Table 7). The most remarkable find was a small disjunct population of *Asclepias ovalifolia* (dwarf milkweed) (Figure 13) discovered by HMNF surveyors in Yates Township (*D. Gaebel and M. Yageman 1*, MICH). This species was previously known in Michigan only from Menominee County in the Upper Peninsula, but it occurs as far south as southern Iowa in its core Great Plains range (Kartesz 2015). The principally northern *Arceuthobium pusillum* (dwarf mistletoe) and northern (and/or high-elevation) *Oxalis acetosella* (northern wood-sorrel) both occur locally in cold conifer-dominated swamps in the



FIGURE 13. The state-endangered *Asclepias ovalifolia* (dwarf milkweed), thought to be restricted to Menominee County in the Upper Peninsula until its recent discovery in Yates Township in Lake County. Photo by B. S. Slaughter, Menominee Co., Michigan.

northern townships (Table 7). Several other species at or near their extant southern range limits were encountered on cool riverbanks and wooded slopes adjacent to swamps. Among these were *Cynoglossum boreale* (northern wild comfrey), *Equisetum pratense* (meadow horsetail), *Lonicera hirsuta* (hairy honeysuckle), and *Petasites frigidus* (sweet-coltsfoot). The northern conifer *Abies balsamea* (balsam fir) appears to be scarce outside of a small area where Lake, Osceola, and Wexford counties adjoin⁶. Further surveys are needed to clarify the abundance and distribution of these and other principally northern species within the county.

Non-native and Invasive Species

When we initiated our study in 2013, approximately 10% of the vascular flora vouchered from Lake County was comprised of non-native species, ranking lowest among Michigan counties in that respect (MICHIGAN FLORA ONLINE

⁶ *Abies balsamea* is almost entirely restricted to northern Michigan, with one outlying collection from a bog in Ingham County (MICHIGAN FLORA ONLINE 2011). Just east and north of Lake County, *A. balsamea* and *Picea mariana* (black spruce), the latter nearly restricted to acidic bogs in Lake County, mingle with *Thuja occidentalis* (northern white-cedar) over extensive tracts. These cold, dark, moss-carpeted swamps beckon and charm seekers of botanical treasures but are unfortunately themselves elusive in Lake County, presumably due to the relatively warm climate and perhaps human disturbance.

2011; Voss and Reznicek 2012). Our collections markedly closed that collection gap, increasing the relative proportion of non-native flora to 20% (Table 4)⁷. A few non-native invasive species are particularly abundant within Lake County on dry, open or semi-shaded sandy soils. From a stewardship perspective, the most troublesome examples include *Centaurea stoebe* (spotted knapweed), *Elaeagnus umbellata* (autumn-olive), *Euphorbia virgata* (leafy spurge), *Lonicera ×bella* (hybrid honeysuckle), *L. morrowii* (Morrow honeysuckle), *Melilotus albus* (white sweet-clover), *M. officinalis* (yellow sweet-clover), and *Securigera varia* (crown-vetch). Species typical of cultivated ground or urban areas, such as *Abutilon theophrasti* (velvet-leaf), *Brassica rapa* (field mustard), *Datura stramonium* (jimson-weed), *Draba verna* (whitlow-grass), *Eragrostis cilianensis* (stink grass), *Lamium purpureum* (purple dead-nettle), and *Thlaspi arvense* (penny cress) occurred more locally, usually on heavier soils (e.g., in Chase Township) and in waste areas and near structures, as at Baldwin.

Many of Michigan's most destructive invasive plants are uncommon within Lake County. Examples among our collections include *Celastrus orbiculatus* (Oriental bittersweet), *Phragmites australis* subsp. *australis* (reed), *Rhamnus cathartica* (common buckthorn), *Rosa multiflora* (multiflora rose), and *Typha angustifolia* (narrow-leaved cat-tail). We observed only a few localized populations of *Alliaria petiolata* (garlic mustard), but dozens of stations are reported on the Midwest Invasive Species Information Network (MISIN 2019) and Early Detection & Distribution Mapping System (EDDMapS 2019). *Frangula alnus* (glossy buckthorn) was not observed and has not been reported from Lake County as of early 2019 on either of these websites, but its presence in adjacent counties suggests its furtive residence.

CONCLUSIONS

Prior to the unveiling of MICHIGAN FLORA ONLINE (2011), compiling county-level species lists and identifying unvouchered targets involved manual examination of dated county maps in *Michigan Flora* (Voss 1972, 1985, 1996). Now, botanists have access to regularly updated species treatments, maps, and specimen data that greatly enhance our ability to address collection gaps. While our examination of the Lake County flora is incomplete, we were able to add hundreds of new species records that considerably improve our understanding of its vegetation and flora. Additional exploration and collecting focused on new records and resolution of species ranges and abundances within the county is recommended, as is coordination among herbaria to ensure that existing but unverified specimens are examined for inclusion in MICHIGAN FLORA ON-

⁷ For perspective, non-native species comprise approximately 37.5% of the Michigan Flora (MICHIGAN FLORA ONLINE 2011). At the county level, the proportion of non-native species ranges from 11% (Wexford County) to 32% (Washtenaw and Wayne counties), indicative of both collection bias and the large number of non-native species represented by one or few populations, these often transient.

LINE. Trowels, field presses, and their human assistants should also be directed to other poorly-collected counties, especially the contiguous three-county area of Osceola, Missaukee, and Wexford. The paucity of specimens from interior northern Lower Michigan is, reciprocally, an opportunity for discovery.

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APPENDIX 1. CHECKLIST OF VASCULAR PLANTS NEWLY CONFIRMED FOR LAKE COUNTY

The following checklist is arranged phylogenetically by major clade or group and then alphabetically by family, genus and species. Classes, subclasses, orders, and family circumscriptions for pteridophytes follow PPG I (2016); conifer subclass and family circumscriptions follow Chase and Reveal (2009) and MICHIGAN FLORA ONLINE (2011), respectively; and major angiosperm clades and grades and family circumscriptions follow APG IV (2016). Families treated in MICHIGAN FLORA ONLINE (2011) that are not treated in APG IV are included and cross-referenced in the checklist. Genera and species follow MICHIGAN FLORA ONLINE (2011). This checklist is limited to species that are newly confirmed for Lake County and substantiated with our specimens. The full list of vouchered taxa known from the county is searchable on MICHIGAN FLORA ONLINE (2011).

Each checklist entry includes the scientific name in *italics*, followed by the authority for the name, the common name, and, in parentheses, collector initial (K = Amanda K. Klain; S = Bradford S. Slaughter), and collection number. Introduced species are indicated with an asterisk (*) preceding the scientific name. Species lacking an asterisk are considered native to Michigan (MICHIGAN FLORA ONLINE 2011) but are not necessarily native to Lake County (e.g., *Gymnocladus dioica*). Species listed as Endangered, Threatened, or Special Concern in Michigan (following MNFI 2009) are denoted by the listing category in **BOLD CAPITALS** following the collection numbers. All collections were deposited at The University of Michigan Herbarium (MICH). Location, population, and habitat data are not provided in the checklist but are searchable (or will become searchable with future updates) on MICHIGAN FLORA ONLINE (2011).

LYCOPODIALES (Lycopods)

LYCOPODIACEAE

- Dendrolycopodium hickeyi* (W. H. Wagner, Beitel & R. C. Moran) A. Haines (S2005)
Diphasiastrum digitatum (A. Braun) Holub, ground-cedar (S1334)

Lycopodium clavatum L., running ground-pine (S1336)
Spinulum annotinum (L.) A. Haines, stiff clubmoss (S1644)

EQUISETIDAE (Horsetails)

EQUISETACEAE

Equisetum arvense L., common horsetail (K177, S1263)
Equisetum fluviatile L., water horsetail (S1793)
Equisetum laevigatum A. Braun, smooth scouring rush (S1654)
Equisetum pratense Ehrh., meadow horsetail (S1260)
Equisetum scirpoides Michx., dwarf scouring rush (S1400)
Equisetum sylvaticum L., woodland horsetail (S1127)

POLYPODIIDAE (Leptosporangiate Ferns)

ASPLENIACEAE

Asplenium platyneuron (L.) D. C. Eaton, ebony spleenwort (S1621)

ATHYRIACEAE

Athyrium filix-femina (L.) Roth, lady fern (S1495)
Deparia acrostichoides (Michx.) Desv., silvery spleenwort (S1953)

CYSTOPTERIDACEAE

Cystopteris bulbifera (L.) Bernh., bulblet fern (S1254)
Gymnocarpium dryopteris (L.) Newm., oak fern (S1241)

DRYOPTERIDACEAE

Dryopteris cristata (L.) A. Gray, crested shield fern (S1463)
Polystichum acrostichoides (Michx.) Schott., Christmas fern (S1200)

ONOCLEACEAE

Matteuccia struthiopteris (L.) Todaro, ostrich fern (S1415)
Onoclea sensibilis L., sensitive fern (S1267)

OSMUNDACEAE

Osmunda claytoniana L., interrupted fern (S1424)
Osmunda regalis L., royal fern (S1476)

THELYPTERIDACEAE

Thelypteris noveboracensis (L.) Nieuwl., New York fern (S1692)
Thelypteris palustris Schott., marsh fern (S1690)

PINIDAE (Conifers)

CUPRESSACEAE

Juniperus communis L., common juniper (S1935)
Juniperus virginiana L., red-cedar (K404)

PINACEAE

Abies balsamea (L.) Mill., balsam fir (S1797)
**Picea abies* (L.) H. Karst., Norway spruce (S2284)
Pinus strobus L., white pine (K218)
**Pinus sylvestris* L., Scots pine (S1623)

BASAL ANGIOSPERMS

CABOMBACEAE

Brasenia schreberi J. F. Gmel., water-shield (S1706)

MAGNOLIIDAE (Magnoliids)

ARISTOLOCHIACEAE

Asarum canadense L., wild-ginger (S1399)

LAURACEAE

Lindera benzoin (L.) Blume, spicebush (S1800)

MONOCOTS

ALISMATACEAE

- Alisma triviale* Pursh, northern water-plantain (S1911, 1961)
Sagittaria latifolia Willd., wapato (S1729)

AMARYLLIDACEAE

- Allium canadense* L., wild garlic (S1138, 1192)
**Narcissus pseudonarcissus* L., daffodil (S2004)

ARACEAE

- Calla palustris* L., wild calla (S1489)
Lemna minor L., common duckweed (S1901)
Lemna turionifera Landolt, red duckweed (S1642)
Symplocarpus foetidus (L.) Nutt., skunk-cabbage (S1384)
Wolffia columbiana H. Karst., common water meal (S2286)

ASPARAGACEAE

- **Asparagus officinalis* L., garden asparagus (S1490)
**Convallaria majalis* L., lily-of-the-valley (S1790)
Maianthemum canadense Desf., Canada mayflower (S1142)
Maianthemum racemosum (L.) Link, false spikenard (S1166, 1266)
Maianthemum stellatum (L.) Link, starry false Solomon-seal (S1137)
Maianthemum trifolium (L.) Sloboda, false mayflower (S2285)
**Muscari neglectum* Tenore, grape-hyacinth (S1386, 1769)
Uvularia grandiflora Sm., bellwort (S1261)

ASPHODELACEAE

- **Hemerocallis fulva* (L.) L., orange day-lily (S1876)
**Hemerocallis lilio-asphodelus* L., yellow day-lily (S1820)

CONVALLARIACEAE—SEE ASPARAGACEAE

CYPERACEAE

- Carex adusta* Boott, sedge (S1666)
Carex albicans Spreng. var. *emmonsii* (Torr.) Rettig, sedge (S1633)
Carex albursina E. Sheld., sedge (S1613)
Carex alopecoidea Tuck., sedge (S2235)
Carex arctata Boott, sedge (S1410)
Carex argyrantha Tuck., sedge (S1997)
Carex aurea Nutt., sedge (S1242)
Carex blanda Dewey, sedge (S2210)
Carex brevior (Dewey) Mack., sedge (S1867)
Carex bromoides Willd., sedge (S1194)
Carex brunnescens (Pers.) Poir., sedge (S1643)
Carex buxbaumii Wahlenb., sedge (S1669)
Carex canescens L., sedge (S1635)
Carex castanea Wahlenb., sedge (S1630, 1814)
Carex cephaloidea (Dewey) Dewey, sedge (S1431)
Carex comosa Boott, sedge (S1686)
Carex crinita Lam., sedge (S1190, 1634)
Carex cristatella Britton, sedge (S1196)
Carex debilis Michx. var. *rudgei* L. H. Bailey, swamp sedge (S1631)
Carex deweyana Schwein., sedge (S1201)
Carex diandra Schrank, sedge (S1652)
Carex disperma Dewey, sedge (S1234)
Carex flava L., sedge (S1236)
Carex gracillima Schwein., sedge (S1188)
Carex granularis Willd., sedge (S1649)
Carex grisea Wahlenb., sedge (S1191)
Carex hirtifolia Mack., sedge (S1763)

- Carex hitchcockiana* Dewey, sedge (S1612)
Carex hystericina Willd., sedge (S1233)
Carex interior L. H. Bailey, sedge (S1129)
Carex lacustris Willd., sedge (S1601)
Carex laevivaginata (Kük.) Mack., sedge (S1817)
Carex laxiculmis Schwein. var. *copulata* (L. H. Bailey) Fernald, sedge (S1202)
Carex laxiflora Lam., sedge (S1404)
Carex leptalea Wahlenb., sedge (S1235)
Carex leptonervia (Fernald) Fernald, sedge (S1620)
Carex lucorum Link, sedge (S1834)
Carex lurida Wahlenb., sedge (S2290)
Carex pallescens L., pale sedge (S1826)
Carex peckii Howe, sedge (S1414)
Carex pedunculata Willd., sedge (S1398)
Carex pennsylvanica Lam., sedge (S1099, 1104, 1629)
Carex plantaginea Lam., sedge (S1427)
Carex prairea Dewey, sedge (S1239)
Carex prasina Wahlenb., sedge (S1794)
Carex projecta Mack., sedge (S1657, 1661, 1700, 1887)
Carex pseudocyperus L., sedge (S1482)
Carex radiata (Wahlenb.) Small, straight-styled wood sedge (S1193, 1798)
Carex retrorsa Schwein., sedge (S1659)
Carex scabrata Schwein., sedge (S1244)
Carex schweinitzii Schwein., sedge (S1815)
Carex scoparia Willd., sedge (S1670, 1672)
Carex siccata Dewey, sedge (S1591)
Carex sparganioides Willd., sedge (S1199)
Carex sprengelii Spreng., sedge (S1402)
Carex stipata Willd., sedge (S1198)
Carex stricta Lam., sedge (S1268, 1606)
Carex tenera Dewey, sedge (S1671, 1835)
Carex tuckermanii Dewey, sedge (S1253)
Carex utriculata Boott, sedge (S1811)
Carex woodii Dewey, sedge (S1796)
Cladium mariscoides (Muhl.) Torr., twig-rush (S1226)
Cyperus schweinitzii Torr., rough sand sedge (K402, S1923)
Cyperus strigosus L., long scaled nut sedge (S1956)
Eleocharis elliptica Kunth, golden-seeded spike-rush (S1339)
Eleocharis engelmannii Steud., Engelmann's spike-rush (S1382). **SPECIAL CONCERN**
Eleocharis erythropoda Steud., spike-rush (S1728)
Eleocharis intermedia Schult., spike-rush (S2549)
Eleocharis obtusa (Willd.) Schult., spike-rush (S1885)
Eleocharis robbinsii Oakes, spike-rush (S1931)
Eleocharis rostellata Torr., beaked spike-rush (S1331)
Eriophorum gracile W. D. J. Koch, slender cotton-grass (S1603)
Rhynchospora fusca (L.) W. T. Aiton, beak-rush (S1608)
Rhynchospora macrostachya A. Gray, tall beak-rush (S1315). **SPECIAL CONCERN**
Schoenoplectus pungens (Vahl) Palla, three-square (S1328)
Scirpus atrovirens Willd., bulrush (S1487)
Scirpus pendulus Muhl., bulrush (S1645)
Scleria pauciflora Willd. var. *pauciflora*, few-flowered nut-rush (S1312). **ENDANGERED**
Scleria triglomerata Michx., tall nut-rush (S1311). **SPECIAL CONCERN**

DIOSCOREACEAE

- Dioscorea villosa* L., wild yam (S1262)

HYACINTHACEAE—SEE ASPARAGACEAE

HYDROCHARITACEAE

Elodea canadensis Michx., common waterweed (S1387)

IRIDACEAE

**Iris germanica* L., flag (S1627)

Iris versicolor L., wild blue flag (S1650)

Sisyrinchium montanum Greene var. *crebrum* Fernald, mountain blue-eyed-grass (S1830)

Sisyrinchium mucronatum Michx., slender blue-eyed-grass (S1647)

Sisyrinchium strictum E. P. Bicknell, blue-eyed-grass (S1154, 1223, 1596). **SPECIAL CONCERN**

JUNCACEAE

Juncus articulatus L., jointed rush (S1926)

Juncus balticus Willd. subsp. *littoralis* (Engelm.) Snogerup., Baltic rush (S1222)

Juncus bufonius L. var. *bufonius*, toad rush (S1914)

Juncus nodosus L., knotted rush (S1240)

Juncus pylaei Laharpe, Pylaei's soft rush (S1460, 1730, 1869)

Juncus tenuis Willd., path rush (K142)

Juncus torreyi Coville, Torrey's rush (S1973)

Luzula multiflora (Ehrh.) Lej., common wood rush (S1825)

LILIACEAE

Lilium michiganense Farw., Michigan lily (S1256)

Medeola virginiana L., Indian cucumber-root (S1632)

MELANTHIACEAE

Alettris farinosa L., colic root (S2403)

Trillium cernuum L., nodding trillium (S1405)

ORCHIDACEAE

Arethusa bulbosa L., dragon's mouth (S1605)

Corallorhiza odontorhiza (Willd.) Nutt., fall coral-root (S1337)

Cypripedium reginae Walter, showy lady-slipper (S1187)

**Epipactis helleborine* (L.) Crantz, helleborine (S1272)

Liparis loeselii (L.) Rich., Loesel's twayblade (S1898)

POACEAE

**Agrostis gigantea* Roth, redtop (S1473)

Agrostis perennans (Walter) Tuck., autumn bent (S1977)

Agrostis scabra Willd., ticklegrass (S1045)

Alopecurus aequalis Sobol., short-awned foxtail (S1641)

Andropogon virginicus L., broom-sedge (S2001)

**Anthoxanthum odoratum* L., sweet vernal grass (S1818)

Aristida basiramea Vasey, fork-tipped three-awned grass (S1044)

Aristida purpurascens Poir., three-awned grass (S2000)

**Bromus japonicus* Murray, Japanese brome (K158, 391; S1247)

Bromus latiglumis (Shear) Hitchc., ear-leaved brome (S1494)

Bromus nottowanus Fernald, satin brome (S1465)

**Bromus squarrosus* L., brome (S1889)

**Bromus tectorum* L., soft chess (S1805)

Cinna arundinacea L., wood reedgrass (S1732)

Cinna latifolia (Goepp.) Griseb., wood reedgrass (S1504)

**Dactylis glomerata* L., orchard grass (S1445)

Dichanthelium clandestinum (L.) Gould, panic grass (S2240)

Dichanthelium commutatum (Schult.) Gould subsp. *ashei* (Ashe) Fernald, panic grass (S1930)

Dichanthelium dichotomum (L.) Gould, panic grass (S1938)

Dichanthelium spretum (Schult.) Freckmann, Eaton's rosette grass (S1316)

Digitaria cognata (Schult.) Pilg., fall witch grass (S1975)

**Digitaria ischaemum* (Schreb.) Muhl., smooth crab grass (S1734)

- Echinochloa muricata* (P. Beauv.) Fernald var. *microstachya* Wiegand, barnyard grass (S1989)
- **Elymus repens* (L.) Gould, quack grass (S1656)
- Elymus riparius* Wiegand, riverbank wild-rye (S1496)
- Elymus virginicus* L., Virginia wild-rye (S1493)
- **Eragrostis cilianensis* (All.) Janch., stink grass (S1992)
- Eragrostis hypnoides* (Lam.) Britton, Sterns & Poggenb., creeping love grass (S2548)
- **Eragrostis minor* Host, low love grass (S1846)
- Eragrostis pectinacea* (Michx.) Nees, love grass (S1048)
- Eragrostis spectabilis* (Pursh) Steud., purple love grass (S1047)
- **Festuca rubra* L., red fescue (S2236)
- Festuca subverticillata* (Pers.) E. B. Alexeev, nodding fescue (S1702)
- **Festuca trachyphylla* (Hack.) Krajina, sheep fescue (S1446)
- Glyceria grandis* S. Watson, reed manna grass (S1471)
- Glyceria septentrionalis* Hitchc., floating manna grass (S1884)
- Glyceria striata* (Lam.) Hitchc., fowl manna grass (S1189)
- Leersia virginica* Willd., white grass (S1736)
- **Lolium perenne* L., ryegrass (S1688)
- Muhlenbergia frondosa* (Poir.) Fernald, common satin grass (S2546)
- Muhlenbergia glomerata* (Willd.) Trin., marsh wild timothy (S1043, 1330)
- Muhlenbergia schreberi* J. F. Gmel., nimblewill (S1947)
- Muhlenbergia sylvatica* Torr., woodland satin grass (S2547)
- Oryzopsis asperifolia* Michx., rough-leaved rice-grass (S1388)
- Panicum dichotomiflorum* Michx., panic grass (S2545)
- Panicum virgatum* L., switch grass (S1737)
- **Phleum pratense* L., timothy (S1655)
- Phragmites australis* (Cav.) Steud. subsp. *americanus* Saltonst., P. M. Peterson & Soreng, reed (S1969)
- **Phragmites australis* (Cav.) Steud. subsp. *australis*, reed (S1951)
- Poa alsodes* A. Gray, grove bluegrass (S1144, 1637, 1810)
- **Poa annua* L., annual bluegrass (S1107)
- **Poa bulbosa* L., bluegrass (S1773)
- **Poa nemoralis* L., bluegrass (S1703)
- Poa saltuensis* Fernald & Wiegand, bluegrass (S1799, 1809)
- **Schedonorus arundinaceus* (Schreb.) Dumort., tall fescue (K141)
- **Secale cereale* L., rye (S1648)
- **Setaria faberi* Herrm., giant foxtail (S1979)
- **Sorghum bicolor* (L.) Moench var. *bicolor*, sorghum (S1988)
- Sphenopholis intermedia* (Rydb.) Rydb., slender wedgegrass (S1701)
- Torreyochloa fernaldii* (Hitchc.) G. L. Church, Fernald's false mannagrass (S2289)
- Tridens flavus* (L.) Hitchc., purpletop (S2544)

POTAMOGETONACEAE

- Potamogeton berchtoldii* Fieber, pondweed (S2288)
- Stuckenia pectinata* (L.) Börner, sago pondweed (K400)

SMILACACEAE

- Smilax ecirrata* (Kunth) S. Watson, upright carrion-flower (S1255)

TRILLIACEAE—SEE MELANTHIACEAE

TYPHACEAE

- Sparganium americanum* Nutt., American bur-reed (S1726)
- Sparganium natans* L., small bur-reed (S1948)
- **Typha angustifolia* L., narrow-leaved cat-tail (S1329)
- Typha latifolia* L., common cat-tail (S1481)

EUDICOTS

ADOXACEAE

- Sambucus racemosa* L., red-berried elder (S1764)

- Viburnum lentago* L., nannyberry (S1425)
**Viburnum opulus* L., European highbush-cranberry (S1829)
Viburnum trilobum Marshall, American highbush-cranberry (K193)

AMARANTHACEAE

- Amaranthus albus* L., tumbleweed (S1968)
**Amaranthus powellii* S. Watson, tall amaranth (S1990)
**Amaranthus retroflexus* L., rough amaranth (S1942)
**Chenopodium album* L., lambs-quarters (S1374, 1919)
**Chenopodium glaucum* L., oak-leaved goosefoot (S1943)
Chenopodium simplex Raf., maple-leaved goosefoot (S1983)

ANACARDIACEAE

- **Cotinus coggygria* Scop., smoke-tree (S1710)
Rhus typhina L., staghorn sumac (K216)

APIACEAE

- Berula erecta* (Huds.) Coville, water-parsnip (S1902). **THREATENED**
Cicuta bulbifera L., water hemlock (S1322)
Cicuta maculata L., water hemlock (S1501)
Cryptotaenia canadensis (L.) DC., honewort (S1693)
Heracleum maximum Bartram, cow-parsnip (S1436)
Osmorhiza claytonii (Michx.) C. B. Clarke, hairy sweet-cicely (S1689)
**Pastinaca sativa* L., wild parsnip (S1877)
Sium suave Walter, water-parsnip (S1883)
**Torilis japonica* (Houtt.) DC., hedge-parsley (K195, S1270)
Toxicodendron radicans (L.) Kuntze, poison-ivy (S1910)

APOCYNACEAE

- Apocynum cannabinum* L. var. *cannabinum*, Indian-hemp (S1904)
**Vinca minor* L., periwinkle (S1767)

ARALIACEAE

- Aralia hispida* Vent., bristly sarsaparilla (S1665)
Aralia nudicaulis L., wild sarsaparilla (S1433)
Hydrocotyle americana L., water-pennywort (K191)

ASTERACEAE

- Achillea millefolium* L., yarrow (S1440)
Ageratina altissima (L.) R. M. King & H. Rob., white snakeroot (S1502)
Antennaria parlinii Fernald, smooth pussytoes (S1103)
**Anthemis arvensis* L., corn chamomile (S1106)
**Arctium minus* Bernh., common burdock (S1880)
**Artemisia ludoviciana* Nutt., western mugwort (S1976)
Bidens discoidea (Torr. & A. Gray) Britton, swamp beggar-ticks (S1998)
Bidens frondosa L., common beggar-ticks (K214)
Bidens vulgata Greene, tall beggar-ticks (S1959)
**Cirsium arvense* (L.) Scop., Canada thistle (S1681)
Cirsium discolor (Willd.) Spreng., pasture thistle (S1915)
**Cirsium vulgare* (Savi) Ten., bull thistle (S1722)
Coreopsis tripteris L., tall coreopsis (S1908)
**Crepis tectorum* L., hawk's beard (S1921)
Doellingeria umbellata (Mill.) Nees, flat-topped white aster (S1327)
Erechtites hieraciifolius (L.) Raf., fireweed (S1318)
Erigeron annuus (L.) Pers., daisy fleabane (S1865, 1936)
Erigeron philadelphicus L., common fleabane (S1141)
Erigeron pulchellus Michx., robin's-plantain (S1134)
Erigeron strigosus Willd., daisy fleabane (S1049)
Helianthus giganteus L., tall sunflower (S2551)
Helianthus hirsutus Raf., hairy sunflower (S1894). **SPECIAL CONCERN.**

- **Hieracium caespitosum* Dumort., king devil (S1592)
- Petasites frigidus* (Aiton) A. Gray var. *palmatus* (Aiton) Cronquist, sweet-coltsfoot (S1246)
- Prenanthes alba* L., white lettuce (S1505)
- Rudbeckia laciniata* L., tall coneflower (S1723)
- Solidago altissima* L., tall goldenrod (S1751)
- Solidago caesia* L., bluestem goldenrod (S1340)
- Solidago flexicaulis* L., zigzag goldenrod (S1982)
- Solidago gigantea* Aiton, late goldenrod (S1324)
- Solidago uliginosa* Nutt., bog goldenrod (S1326)
- **Sonchus arvensis* L., field sow-thistle (S1899)
- Symphotrichum cordifolium* (L.) G. L. Nesom, heart-leaved aster (S1960)
- Symphotrichum novae-angliae* (L.) G. L. Nesom, New England aster (S1972)
- Symphotrichum ontarionis* (Wiegand) G. L. Nesom, Lake Ontario aster (S1981)
- Symphotrichum pilosum* (Willd.) G. L. Nesom var. *pilosum*, frost aster (S1980)
- Symphotrichum puniceum* (L.) Á. Löve & D. Löve, swamp aster (S1727)
- **Tanacetum vulgare* L., common tansy (S1907)
- **Taraxacum officinale* F. H. Wigg., common dandelion (S1385)
- **Tragopogon dubius* Scop., goat's beard (S1600)
- **Tragopogon pratensis* L., common goat's beard (S1599)

BERBERIDACEAE

- **Berberis thunbergii* DC., Japanese barberry (S2006)
- **Berberis vulgaris* L., common barberry (S1813)
- Podophyllum peltatum* L., may-apple (S1426)

BETULACEAE

- Betula alleghaniensis* Britton, yellow birch (S1795)
- Carpinus caroliniana* Walter, blue-beech (K129)
- Corylus americana* Walter, hazelnut (S1638)
- Corylus cornuta* Marshall, beaked hazelnut (S2209)
- Ostrya virginiana* (Mill.) K. Koch, ironwood (S1705)

BIGNONIACEAE

- **Catalpa speciosa* Warder, northern catalpa (S2397)

BORAGINACEAE

- Cynoglossum boreale* Fernald, northern wild comfrey (S1245)
- Hackelia virginiana* (L.) I. M. Johnst., beggar's lice (S1879)
- Hydrophyllum appendiculatum* Michx., great waterleaf (S1614)
- Hydrophyllum canadense* L., Canada waterleaf (S1844)
- Hydrophyllum virginianum* L., Virginia waterleaf (S1803)
- Lithospermum caroliniense* (Walter) MacMill., hairy puccoon (S1167)
- **Myosotis stricta* Link, small-flowered forget-me-not (S1772)
- **Myosotis sylvatica* Hoffm., garden forget-me-not (S1416)

BRASSICACEAE

- **Alliaria petiolata* (M. Bieb.) Cavara & Grande, garlic mustard (S1408)
- **Alyssum alyssoides* (L.) L., pale alyssum (S1112)
- **Barbarea vulgaris* R. Br., yellow rocket (S1131)
- **Brassica rapa* L., field mustard (S1788)
- Cardamine bulbosa* (Muhl.) Britton, Sterns & Poggenb., spring cress (S1139)
- Cardamine concatenata* (Michx.) O. Schwarz, cut-leaved toothwort (S1389)
- Cardamine diphylla* (Michx.) Alph. Wood, two-leaved toothwort (S1403)
- **Cardamine flexuosa* With., bitter cress (S1849)
- Cardamine pensylvanica* Willd., Pennsylvania bitter cress (S1128)
- **Draba verna* L., whitlow-grass (S2003)
- **Hesperis matronalis* L., dame's rocket (S1432)
- **Lunaria annua* L., money-plant (S2007)
- **Nasturtium microphyllum* Rchb., watercress (S2291)
- Nasturtium officinale* W. T. Aiton, watercress (S1238)

**Sisymbrium officinale* L., hedge mustard (S2400)

**Thlaspi arvense* L., penny cress (S1848)

CACTACEAE

Opuntia cespitosa Raf., prickly-pear (S2399)

CAMPANULACEAE

Lobelia inflata L., indian-tobacco (S1733)

Triodanis perfoliata (L.) Nieuwl., Venus's looking-glass (S1847)

CANNABACEAE

Humulus lupulus L., common hops (S1971)

CAPRIFOLIACEAE

Diervilla lonicera Mill., bush-honeysuckle (S1843)

**Dipsacus fullonum* L., wild teasel (S1891)

**Lonicera xbella* Zabel, hybrid honeysuckle (S1126)

Lonicera canadensis Marshall, Canadian fly honeysuckle (S1417)

Lonicera hirsuta Eaton, hairy honeysuckle (S1437)

**Lonicera morrowii* A. Gray, Morrow honeysuckle (S1801)

**Lonicera tatarica* L., Tartarian honeysuckle (S1893)

Symphoricarpos albus (L.) S. F. Blake var. *albus*, snowberry (S1466)

CARYOPHYLLACEAE

**Agrostemma githago* L., corn-cockle (S1252)

**Arenaria serpyllifolia* L., thyme-leaved sandwort (K143, S1109)

Cerastium arvense L., field chickweed (K133, S1096, S1770)

**Cerastium semidecandrum* L., small mouse-ear chickweed (S1108)

**Dianthus armeria* L., Deptford pink (S1685)

**Herniaria glabra* L., herniary (S1866)

**Myosoton aquaticum* (L.) Moench, giant chickweed (S2237)

**Petrorhagia saxifraga* (L.) Link, pink (S1488)

**Scleranthus annuus* L., knawel (S1110)

**Silene latifolia* Poir., white campion (S1441)

Stellaria longifolia Willd., long-leaved chickweed (S1143)

**Stellaria media* (L.) Vill., common chickweed (S1265)

CELASTRACEAE

**Celastrus orbiculatus* Thunb., oriental bittersweet (S2396)

Celastrus scandens L., climbing bittersweet (S1892)

CISTACEAE

Lechea intermedia Britton, intermediate pinweed (S1313)

CLEOMACEAE

Polanisia dodecandra (L.) DC. var. *dodecandra*, clammy-weed (K395, S1918)

CONVOLVULACEAE

Calystegia sepium (L.) R. Br., hedge bindweed (S2239)

Calystegia spithamea (L.) Pursh, low bindweed (S1662)

**Convolvulus arvensis* L., field bindweed (S1598)

CORNACEAE

Cornus alternifolia L. f., alternate-leaved dogwood (S1694)

Cornus amomum Mill. subsp. *obliqua* (Raf.) J. S. Wilson, silky dogwood (S1871)

Cornus foemina Mill., gray dogwood (K163)

CRASSULACEAE

**Sedum acre* L., mossy stonecrop (K152, S1156)

**Sedum album* L., stonecrop (K398)

CUCURBITACEAE

Echinocystis lobata (Michx.) Torr. & A. Gray, wild-cucumber (S1492)

DIERVILLACEAE—SEE CAPRIFOLIACEAE

DIPSACACEAE—SEE CAPRIFOLIACEAE

ELAEAGNACEAE

**Elaeagnus umbellata* Thunb., autumn-olive (S1420)

ERICACEAE

Chimaphila umbellata (L.) Nutt., pipsissewa (S1216)

Gaultheria hispidula (L.) Bigelow, creeping-snowberry (S1422)

Hypopitys monotropa Crantz, pinesap (S1937)

Orthilia secunda (L.) House, one-sided pyrola (S1464)

Vaccinium myrtilloides Michx., velvetleaf blueberry (S1421)

EUPHORBIACEAE

Acalypha rhomboidea Raf., three-seeded mercury (S1941, 1955)

**Euphorbia cyparissias* L., cypress spurge (S1125)

**Euphorbia glyptosperma* Engelm., ridge-seeded spurge (S1895)

**Euphorbia virgata* Waldst. & Kit., leafy spurge (S1132)

FABACEAE

Apios americana Medik., groundnut (S2553)

Desmodium canadense (L.) DC., showy tick-trefoil (S1916)

Desmodium illinoense A. Gray, prairie tick-trefoil (S2395)

Desmodium paniculatum (L.) DC., panicle tick-trefoil (S1886)

Desmodium rotundifolium DC., round-leaved tick-trefoil (S1944)

Gleditsia triacanthos L., honey locust (S2554)

Hylodesmum glutinosum (Willd.) H. Ohashi & R. R. Mill, clustered-leaved tick-trefoil (S1257)

Hylodesmum nudiflorum (L.) H. Ohashi & R. R. Mill, naked tick-trefoil (S1888)

**Lathyrus latifolius* L., everlasting pea (S1273)

Lathyrus ochroleucus Hook., pale vetchling (S2212)

Lathyrus palustris L., marsh pea (S2238)

**Lathyrus sylvestris* L., perennial pea (S1462)

Lespedeza hirta (L.) Hornem., hairy bush-clover (S1333)

Lespedeza violacea (L.) Pers., bush-clover (S1946)

**Lotus corniculatus* L., birdfoot trefoil (S1682)

**Medicago sativa* L., alfalfa (S1687)

**Melilotus albus* Medik., white sweet-clover (S1480)

**Melilotus officinalis* (L.) Pall., yellow sweet-clover (S1479)

**Robinia hispida* L., bristly locust (S1610)

**Robinia pseudoacacia* L., black locust (S1622)

**Securigera varia* (L.) Lassen, crown-vetch (S1474)

**Trifolium arvense* L., rabbitfoot clover (S1626)

**Trifolium aureum* Pollich, hop clover (K363)

**Trifolium pratense* L., red clover (S1499)

**Trifolium repens* L., white clover (K156)

Vicia americana Willd., American vetch (S1155, 1442)

**Vicia tetrasperma* (L.) Schreb., sparrow vetch (S1639)

FAGACEAE

Fagus grandifolia Ehrh., American beech (S1617)

Quercus alba L., white oak (S1130)

Quercus macrocarpa Michx., bur oak (S1699)

Quercus rubra L., red oak (S1713)

GERANIACEAE

**Erodium cicutarium* (L.) L'Hér, stork's-bill (S1124)

Geranium maculatum L., wild geranium (S1133)

**Geranium pusillum* L., small geranium (S1806)

Geranium robertianum L., herb Robert (S1435)

GROSSULARIACEAE

Ribes americanum Mill., wild black currant (S1406)

Ribes triste Pall., swamp red currant (S1418)

HALORAGACEAE

Myriophyllum sibiricum Komarov, spiked water-milfoil (S1929)

Proserpinaca palustris L., mermaid-weed (S1483)

HYPERICACEAE

Hypericum punctatum Lam., spotted St. John's-wort (S1477)

JUGLANDACEAE

Carya cordiformis (Wang.) K. Koch, bitternut hickory (S1673)

Juglans nigra L., black walnut (S1684)

LAMIACEAE

**Ajuga reptans* L., carpet bugle (S2211)

**Glechoma hederacea* L., ground-ivy (S1412)

Hedeoma hispida Pursh, rough pennyroyal (S1833)

**Lamium galeobdolon* (L.) Ehrend. & Polatschek, yellow archangel (S1903)

**Lamium purpureum* L., purple dead-nettle (S1549)

**Mentha ×piperita* L., peppermint (S1909)

**Origanum vulgare* L., oregano (S1906)

Pycnanthemum verticillatum (Michx.) Pers., whorled mountain mint (K392). **SPECIAL CONCERN**

Pycnanthemum virginianum (L.) Durand & Jackson, common mountain mint (S1708)

LENTIBULARIACEAE

Utricularia intermedia Hayne, flat-leaved bladderwort (S1335)

Utricularia minor L., small bladderwort (S1927)

Utricularia purpurea Walter, purple bladderwort (S1707)

Utricularia vulgaris L., common bladderwort (S1484)

LYTHRACEAE

**Lythrum salicaria* L., purple loosestrife (S1945)

Rotala ramosior (L.) Koehne, tooth-cup (S1319)

MALVACEAE

**Abutilon theophrasti* Medik., velvet-leaf (S1939)

**Malva neglecta* Wallr., common mallow (S1597)

Tilia americana L., basswood (S1203)

MENISPERMACEAE

Menispermum canadense L., moonseed (S1434)

MENYANTHACEAE

Menyanthes trifoliata L., bogbean (S1604)

MOLLUGINACEAE

**Mollugo verticillata* L., carpetweed (S1046)

MYRICACEAE

Myrica gale L., sweet gale (S1607)

MYRSINACEAE

**Lysimachia nummularia* L., moneywort (K173, S1204)

Lysimachia thyrsoiflora L., tufted loosestrife (S1197)

OLEACEAE

Fraxinus americana L., white ash (S1819)

Fraxinus nigra Marshall, black ash (K204)

Fraxinus pennsylvanica Marshall, green ash (S1205, 1711)

**Syringa vulgaris* L., common lilac (K361)

ONAGRACEAE

- Circaea canadensis* (L.) Hill, enchanter's-nightshade (S1258)
**Epilobium hirsutum* L., great hairy willow-herb (S1500)
Epilobium leptophyllum Raf., fen willow-herb (S1332)
**Epilobium parviflorum* Schreb., willow-herb (S1900)
Ludwigia palustris (L.) Elliott, water-purslane (S1724)

OROHACEAE

- Agalinis tenuifolia* (M. Vahl) Raf., common false foxglove (S1962)
Conopholis americana (L.) Wallr., squaw-root (S1832)
Epifagus virginiana (L.) Bart., beech-drops (S1957)
Pedicularis canadensis L., wood-betony (S1123)
Pedicularis lanceolata Michx., swamp-betony (S2552)

OXALIDACEAE

- Oxalis acetosella* L., northern wood-sorrel (S1447)
**Oxalis dillenii* Jacq., common yellow wood-sorrel (K128)

PAPAVERACEAE

- **Chelidonium majus* L., celandine (S1822)
**Papaver orientale* L., Oriental poppy (S1827)

PENTHORACEAE

- Penthorum sedoides* L., ditch stonecrop (S1954)

PHRYMACEAE

- Mimulus ringens* L., monkey-flower (S1461)
Phryma leptostachya L., lopseed (S1878)

PHYTOLACCACEAE

- Phytolacca americana* L., pokeweed (S1864)

PLANTAGINACEAE

- **Chaenorhinum minus* (L.) Lange, dwarf-snapdragon (S1920)
Gratiola neglecta Torr., clammy hedge hyssop (S1668)
Penstemon hirsutus (L.) Willd., hairy beard-tongue (K147a)
**Plantago aristata* Michx., bracted plantain (S2398)
Veronica anagallis-aquatica L., water speedwell (S1704)
**Veronica arvensis* L., field speedwell (S1785)
**Veronica officinalis* L., common speedwell (K167)
Veronica peregrina L., purslane speedwell (S1787)
**Veronica verna* L., spring corn speedwell (S1111, 1771)

POLEMONIACEAE

- Phlox divaricata* L., wild blue phlox (S1140)
**Phlox subulata* L., moss-pink (S1768, 1791)

POLYGONACEAE

- Fallopia cilinodis* (Michx.) Holub, fringed false buckwheat (S1438)
**Fallopia convolvulus* (L.) Á. Löve, black-bindweed (S1868)
**Fallopia japonica* (Houtt.) Ronse Decr., Japanese knotweed (S1823)
Persicaria hydropiper (L.) Delabare, water-pepper (S1932)
Persicaria hydropiperoides (Michx.) Small, mild water-pepper (S1725)
**Persicaria maculosa* Gray, lady's-thumb (S1913)
Persicaria sagittata (L.) H. Gross, arrow-leaved tear-thumb (S1731)
Persicaria virginiana (L.) Gaertn., jumpseed (S1958)
**Polygonum aviculare* L., knotweed (S1343)
**Rumex acetosella* L., sheep sorrel (K161, S1100)
**Rumex crispus* L., curly dock (S1863)
**Rumex obtusifolius* L., bitter dock (S1470)
Rumex orbiculatus A. Gray, great water dock (S1974)

PORTULACACEAE

Portulaca oleracea L., purslane (S1897)

RANUNCULACEAE

Actaea pachypoda Elliott, white baneberry (S1845)

Actaea rubra (Aiton) Willd., red baneberry (S1498)

Anemone canadensis L., Canada anemone (S1269)

Enemion biternatum Raf., false rue-anemone (S1762)

**Ranunculus acris* L., common buttercup (S1430)

Ranunculus fascicularis Bigelow, early buttercup (S1548)

Ranunculus flabellaris Raf., yellow water crowfoot (S1812)

Ranunculus hispidus Michx. var. *caricetorum* (Greene) T. Duncan, swamp buttercup (S1135)

Ranunculus recurvatus Poir., hooked crowfoot (S1136)

Ranunculus sceleratus L., cursed crowfoot (S1999)

Thalictrum dioicum L., early meadow-rue (S1391)

RHAMNACEAE

**Rhamnus cathartica* L., common buckthorn (S1618)

ROSACEAE

Agrimonia gryposepala Wallr., tall agrimony (S1491)

Agrimonia pubescens Wallr., soft agrimony (S1978)

Amelanchier arborea (F. Michx.) Fernald, juneberry (S1541)

Amelanchier interior (Pursh) DC., round-leaved serviceberry (S1401)

Amelanchier spicata (Lam.) K. Koch, shadbush serviceberry (S1098)

Comarum palustre L., marsh cinquefoil (S1224)

Crataegus punctata Jacq., dotted hawthorn (K207)

Geum aleppicum Jacq., yellow avens (S1237)

**Malus pumila* Mill., apple (S1792)

Prunus americana Marshall, American wild plum (K208)

Prunus nigra Aiton, Canada plum (K130)

Prunus virginiana L., choke cherry (S1105)

Rosa blanda Aiton, wild rose (S1443)

**Rosa cinnamomea* L., cinnamon rose (S1828)

**Rosa multiflora* Murray, multiflora rose (S1870)

Rubus allegheniensis Porter, common blackberry (S1615)

Rubus occidentalis L., black raspberry (S1619)

Sibbaldiopsis tridentata (Aiton) Rydb., three-toothed cinquefoil (S1628)

RUBIACEAE

Galium circaezans Michx., white wild licorice (S1264)

Galium obtusum Bigelow, wild madder (S1698)

Galium trifidum L., small bedstraw (S1949)

RUTACEAE

Zanthoxylum americanum Mill., prickly-ash (S1259)

SALICACEAE

**Populus alba* L., white poplar (S1695)

Populus deltoides Marshall, cottonwood (S1824)

Populus grandidentata Michx., big-tooth aspen (S1712)

**Populus nigra* L., Lombardy poplar (S1714)

Salix amygdaloides Andersson, peach-leaved willow (S1653)

Salix bebbiana Sarg., beaked willow (S1970)

Salix eriocephala Michx., heart-leaved willow (S1468)

Salix lucida Muhl., shining willow (S1407, 1469)

Salix petiolaris Sm., slender willow (S1485)

SAPINDACEAE

Acer negundo L., box-elder (S1411)

Acer rubrum L., red maple (S1122)

- Acer saccharinum* L., silver maple (S1145)
Acer saccharum Marshall, sugar maple (S1611)

SARRACENIACEAE

- Sarracenia purpurea* L., pitcher-plant (S1227)

SAXIFRAGACEAE

- Chrysosplenium americanum* Hook., golden saxifrage (S1423)
Micranthes pensylvanica (L.) Haw., swamp saxifrage (S1816)
Mitella nuda L., naked miterwort (S1243)

SOLANACEAE

- **Datura stramonium* L., jimson-weed (S1991)
Physalis heterophylla Nees, clammy ground-cherry (S1625)
**Solanum carolinense* L., horse-nettle (S1933)
**Solanum dulcamara* L., bittersweet nightshade (S1439)
Solanum ptychanthum Dunal, black nightshade (S1940)

THEOPHRASTACEAE

- Samolus parviflorus* Raf., water-pimpernel (S2550)

ULMACEAE

- Ulmus americana* L., American elm (S1691)
**Ulmus pumila* L., Siberian elm (S1804)
Ulmus rubra Muhl., slippery elm (S1802)
Ulmus thomasi Sarg., rock elm (S1784)

URTICACEAE

- Boehmeria cylindrica* (L.) Sw., false nettle (S1321)
Laportea canadensis (L.) Wedd., wood nettle (S1503)
Pilea fontana (Lunell) Rydb., bog clearweed (S1928)
Pilea pumila (L.) A. Gray, clearweed (S1735)
Urtica dioica L., stinging nettle (S1478)

VIOLACEAE

- Viola canadensis* L., Canada violet (S1765)
Viola cucullata Aiton, marsh violet (K157)
**Viola odorata* L., sweet violet (S2002)
Viola rostrata Pursh, long-spurred violet (S1409)
Viola sororia Willd., common blue violet (S1390)

VITACEAE

- Parthenocissus inserta* (A. Kern.) Fritsch, thicket creeper (S1683)
Parthenocissus quinquefolia (L.) Planch., Virginia creeper (S1881)
Vitis aestivalis Michx., summer grape (S1890)
Vitis riparia Michx., river-bank grape (S1429)

DIFFERENTIAL PERSISTENCE AMONG NATIVE SPECIES PLANTED IN A STORMWATER RETENTION POND

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ABSTRACT

Retention ponds are a commonly implemented best management practice to treat urban stormwater. Newly constructed ponds offer an opportunity to increase native plant diversity in these artificial structures. However, plantings are rarely monitored, and shallow water areas often become colonized by non-native, invasive *Typha* spp. We documented the occurrence and abundance of eight planted native macrophytes in a newly constructed retention pond after one growing season and again after six growing seasons. *Typha* species were found in almost all plots after only one growing season and had completely colonized the planted emergent zone after six years. All native planted species, except one, were observed after six growing seasons, albeit at relatively low frequency and low cover. However, *Pontederia cordata* L. and *Scirpus* spp. were observed in over half of the plots, which suggests that they are able to coexist with *Typha* spp. even at low abundances. We suggest that *P. cordata* and *Scirpus* spp. should be considered in plantings in urban retention ponds to increase native species diversity.

KEYWORDS: Macrophytes, Native plants, Restoration, UW-Madison Arboretum

INTRODUCTION

Retention (wet-detention) ponds are a commonly implemented best management practice (BMP) to treat stormwater runoff in urban areas and to protect downstream aquatic systems from nutrient enrichment, sedimentation, toxicity, and reduced biodiversity (Dunn et al. 1995; Marsalek 1998; Tenenbaum 2004; Chen and Adams 2006; Wadzuk et al. 2010; Wang and Sample 2014). In addition, retention ponds can reduce peak flows (Hunt et al. 2008) and can mitigate flooding risk in urban areas (Dunn et al. 1995; Kentula et al. 1992). While they are primarily designed to improve water quality downstream, retention ponds themselves are subject to flashy hydroperiods (Bonilla-Warford and Zedler 2002), turbid water, high levels of soil phosphorus (Hogan and Walbridge 2007), contaminated sediments (Marsalek and Marsalek 1997), and invasion by non-

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native plant species—conditions that are often inhospitable for native plant establishment and use by some wildlife (Bishop et al. 2000a, 2000b).

Retention ponds are designed to store water at stable depths, which reduces the energy of incoming flows and increases the accumulation of sediment-bound phosphorus and toxins. Non-vegetated areas of stormwater ponds are often colonized by non-native invasive plants such as *Typha* spp. (cattail), *Phragmites australis* (common reed), and *Lythrum salicaria* (purple loosestrife) (Schueler 1994; Moore et al. 1999). In particular, the invasive *Typha* × *glauca*, an F1 hybrid between the non-native and invasive *Typha angustifolia* L. (narrow-leaved cattail) and the native *Typha latifolia* L. (broad-leaved cattail) (Smith 1987), has been shown to expand under stable water levels and high nutrient inputs (e.g., Woo and Zedler 2002; Boers and Zedler 2008) making it difficult to increase native plant diversity (Boers et al. 2007).

Despite these disturbances, retention ponds are often planted with native wetland species in an effort to create or restore habitat in these artificial systems. Plant diversity can influence ecosystem properties such as productivity, decomposition rates, nutrient cycling (Engelhardt and Ritchie 2001), and resistance and resilience to disturbance (Hopple and Craft 2013). In addition, plant diversity is positively related to mycorrhizal and insect diversity (Knops et al. 1999). Pier et al. (2015) found that the diversity of the macroinvertebrate community increased after the introduction of 85 native plants to a newly created system of stormwater ponds. However, since constructed wetlands that include native plantings are rarely monitored (Balcombe et al. 2005), this study was undertaken to investigate the disturbance tolerance and competitive ability of eight native macrophytes planted in a newly constructed stormwater retention pond.

METHODS AND MATERIALS

In 2009, a 1.6 ha retention pond was constructed at the University of Wisconsin-Madison Arboretum in Madison, Wisconsin (Figure 1) to treat an average of one hundred and sixty-six million liters (135 acre-feet) of stormwater annually. The pond receives water from a 111 ha urban watershed comprised primarily of residential, commercial, and industrial land uses (University of Wisconsin-Madison Arboretum 2006). The pond edges were graded to insure a relatively consistent water level in the emergent zone (Figure 1). This design allowed the installation of native plants that are appropriate to shallow-water conditions. Plants were purchased from Wildlife Nurseries, Inc. in Oshkosh, Wisconsin approximately 87 miles north-northeast of the study site. All plants were grown from locally collected seed or root stock. In late April and early May of 2010, we planted ninety-six 6 × 1.5 m plots within the pond's emergent zone (Figure 2) with root stocks and bulbs of eight native wetland species: *Acorus calamus* L. (sweet flag), *Bolboschoenus fluviatilis* (Torr) Soják (river bulrush), *Juncus effusus* L. (common rush), *Pontederia cordata* (pickerel-weed), *Sagittaria rigida* Pursh (sessile-fruited arrow-head), *Schoenoplectus acutus* (C.C.Gmel.) Palla (hard-stem bulrush), *Schoenoplectus tabernaemontani* (C.C.Gmel.) Palla (soft-stem bulrush), and *Sparganium eurycarpum* Engelm. (common bur-reed). These species were selected because they are readily available, commonly found in natural and restored wetlands and are often included in species lists for constructed stormwater retention ponds. We randomly assigned each species to one-, three-, or six-species assemblages within plots at a density of 2.7 individuals per m². Each unique monotype or assemblage was assigned to four replicate plots, which in turn were assigned at random within four nearly equal sections of the pond perimeter. We erected chicken-wire fence around the plots in the summer of 2010 to minimize goose herbivory.

In the fall of 2010, and again in 2016, we recorded species presence and percentage cover in all



FIGURE 1. Retention pond study site at the University of Wisconsin-Madison Arboretum, Madison, Wisconsin. Emergent zone and submerged benches are shown in white. Eight native macrophyte species were planted randomly in ninety-six 6× 1.5 m plots within the emergent zone. Image credit: Mark Wegener.

plots. Species percentage cover was recorded in six cover classes, adapted from the Daubenmire scale (Mueller-Dombois and Ellenberg 1974): 1 (0–5%), 2 (6–25%), 3 (26–50%), 4 (51–75%), 5 (76–95%), and 6 (96–100%). For analysis, the categorical cover classes were converted to continuous data by calculating the mid-point of each class. Means are based on the mid-point data. In 2015, the plantings were surveyed using a larger plot size of approximately 3×6 m, which provided a broader picture of the *in situ* emergent plant community that was not focused solely on the original planting area and allowed for an examination of where the emergent plant community became established over time. We present these results separately to provide additional context. For all years, we lumped species of bulrush—*Bulboschoenus fluviatilis*, *Scirpus acutus*, and *Schoenoplectus tabernaemontani*—as “*Scirpus* spp.” because it was difficult to discern between species. *Scirpus* spp. is treated as a single species for analysis purposes. We used paired t-tests to compare the percentage cover of each species between sampling years. Since the ecological management goal of the plantings was to increase native wetland plant diversity, no plots were left as unplanted controls due to the risk of colonization by invasive plants.

In addition to the eight macrophytes, five submergent species were planted in the spring of 2010 on three submerged benches at different water depths at each of six locations around the pond edge (Figure 1). The benches were two, three, and four feet below water level and consisted of a combined total area of 200.94 m², 251.67 m², and 299.43 m², respectively. The five submergent species were: *Elodea canadensis* Michx. (elodea), *Stuckenia pectinata* (L.) Börner (sago pondweed), *Vallisneria americana* Michx. (water celery), *Nymphaea odorata* Aiton (white water-lily), and *Nelumbo lutea* Willd. (American lotus). In order to provide good soil contact and encourage rooting into the substrate (Eleuterius 1975), tubers or seeds were put into a cotton mesh bag with several small rocks and tossed from shore into the appropriate water depth. The bags sank to the pond bottom.



FIGURE 2. Study site at the time of planting in spring 2010. *Typha* spp. is absent. Photo by Brad Herrick.

RESULTS

Within one year after planting, *Typha* spp. was found in 93% of plots, and by 2016 it had invaded all plots (Figures 3 and 4). After six years, all planted species decreased in frequency except *Pontederia cordata*, which showed slight increases between the original planting frequency and subsequent survey events (Figure 4). In 2016, plants with the two highest frequencies were *P. cordata* and *Scirpus* spp., at 66% and 53%, respectively. *Juncus effusus* had the lowest plot frequency, being found in only 2% of plots. *Sparganium eurycarpum* was not detected in surveys after the original planting.

By visual estimation, the clear majority of *Typha* spp. in our plots consisted of *T. × glauca*, although *T. angustifolia* was also present (Galen Smith, personal correspondence). We saw no individuals of *T. latifolia* in our plots or anywhere within the retention pond. Hereafter, *Typha* spp. refers only to *T. × glauca* and *T. angustifolia*.

Between 2010 and 2016, the percentage cover of all planted species except *Pontederia cordata* significantly decreased ($p < 0.05$, Figure 4). *Pontederia cordata* decreased slightly from 8% to 7% but this decrease was not statistically significant ($p = 0.49$). *Typha* spp. significantly increased from 26% to 96% ($p < 0.0001$) over the same time period.

By 2016, 80% of the plots had only one or two planted species present, and



FIGURE 3. Study site at the time of sampling in the fall of 2016. *Typha* spp. have invaded the emergent zone. Photo by Brad Herrick.

an additional 14% of plots were devoid of any planted species. Furthermore, there were no plots by this time with more than three planted species.

Pontederia cordata was the only planted species to increase in plot frequency during the study period; all others decreased (Figure 4). However, all species were present in at least a few plots with the exception of *Sparganium eurycarpum* (Figure 4). In addition, the abundance of *P. cordata* remained relatively stable while all others decreased (Table 1). None of the planted species achieved greater than 9% cover during the study period, likely due to the rapid establishment and increase in cover by *Typha* spp. (Table 1). Planting a higher

TABLE 1. Mean percentage cover of planted native species and invasive *Typha* spp. in 2010 and 2016 (\pm standard deviation) per 6×1.5 m plots. Asterisks represent significant difference between years at $\alpha = 0.05$.

Species	Mean Percentage Cover	
	2010	2016
<i>Acorus calamus</i>	3.85 \pm 0.92	0.45 \pm 0.17*
<i>Juncus effusus</i>	0.23 \pm 0.07	0.05 \pm 0.04*
<i>Pontederia cordata</i>	8.05 \pm 1.53	6.8 \pm 1.25
<i>Sagittaria rigida</i>	0.94 \pm 0.34	0.1 \pm 0.05*
<i>Scirpus</i> spp.	5.05 \pm 0.9	2.21 \pm 0.48*
<i>Sparganium eurycarpum</i>	0	0
<i>Typha</i> spp.	26.48 \pm 3.00	96.46 \pm 0.35*

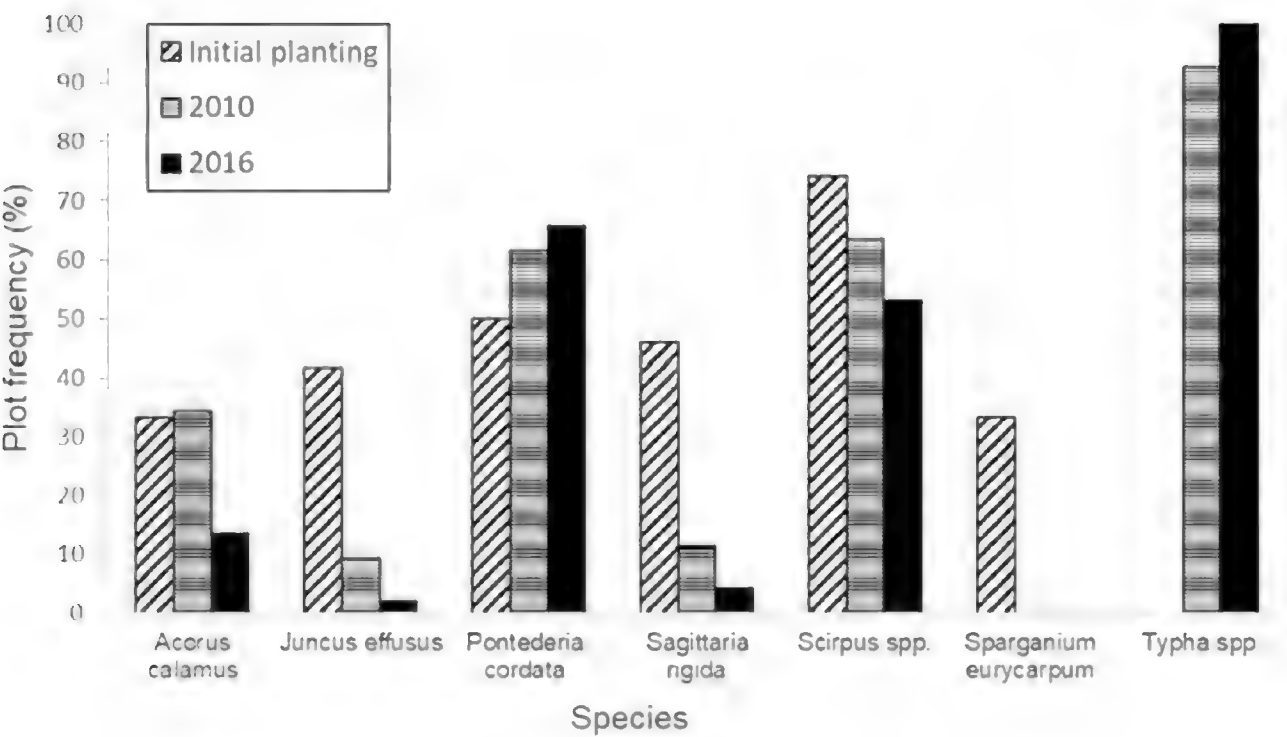


FIGURE 4. Frequency of planted species and *Typha* spp. in 6 x 1.5 m plots at initial planting in 2010 and 2016.

density of native plants, especially *P.cordata* and *Scirpus* spp., may have improved diversity long-term.

2015 data

All planted native species except *Sparganium eurycarpum* were still present in 2015 (Figure 5). *Acorus calamus* was found in 17% of the plots in 2015, as

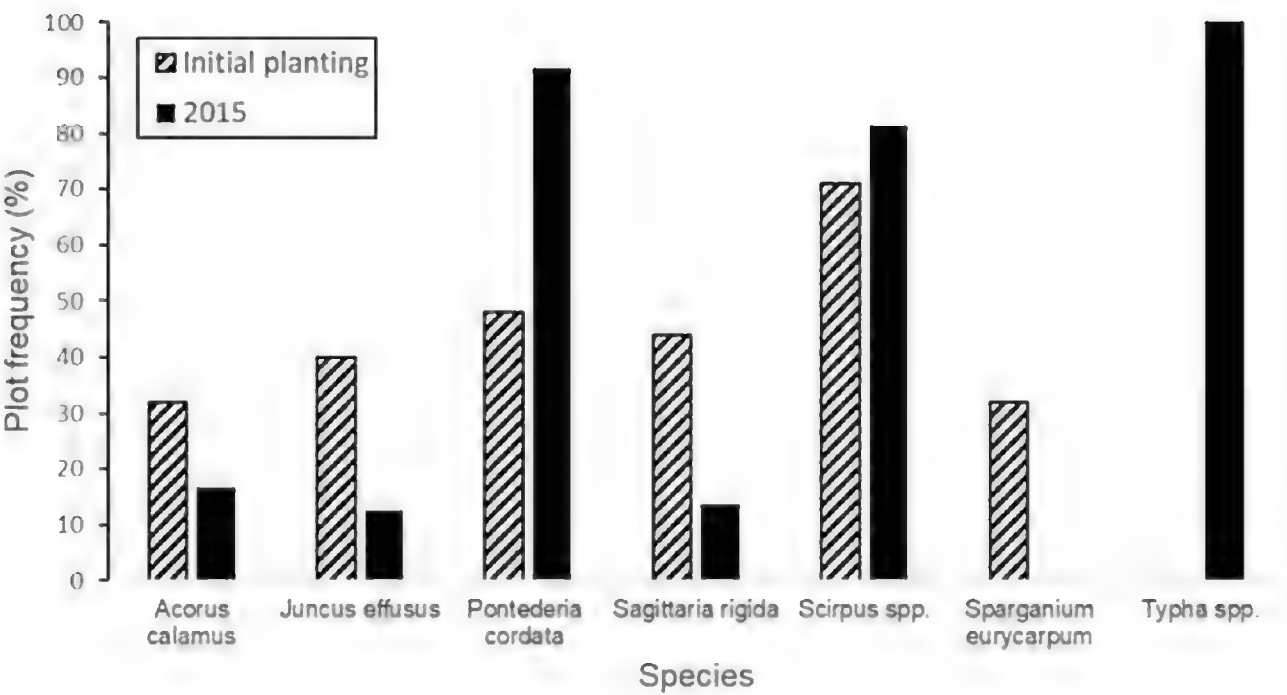


FIGURE 5. Frequency of planted species and *Typha* spp. at the time of planting and in 2015 (6 x 3 m plots).

compared with 14% in 2016. *Juncus effusus* and *S. rigida* were found in 13% and 14% of plots, respectively, in 2015, as compared with 2% and 4% in 2016. Although these three species exhibited increased frequency with a slightly larger sampling unit, percentage cover was similar to that recorded in 2016. Finally, in 2015, *Pontederia cordata* and *Scirpus* spp. were found in 92% and 82% of the plots, respectively, as compared to 66% and 53% in 2016, but with mean cover of just 12% and 7%, respectively.

Planted Submergent Species

Likely due to poor water clarity, none of the planted submergent species were observed in 2016, except for a few scattered patches of *Nymphaea odorata*.

DISCUSSION

We expected *Sparganium eurycarpum* to perform well in a retention pond setting, since it is a robust plant and is often found with *Scirpus* spp. and *Typha* spp. under flooded conditions. Additionally, it has been shown to produce a high amount of above-ground biomass and to reduce competition when planted with other native species (Chapman et al. 2013). However, in our study it was never recorded in surveys after the initial planting. While our data suggest that *S. eurycarpum* may not do well in stormwater retention ponds, we believe that the complete failure of *S. eurycarpum* to establish anywhere within the entire pond as opposed to other planted species obtained from the same nursery and geographic region of Wisconsin, suggests another alternative: that we may have received bad root stock for *S. eurycarpum* or that we planted it incorrectly.

While the invasion of *Typha* × *glauca* was not surprising, due to its establishment throughout the watershed, the likely high levels of nutrients in the pond water and open, shallowly flooded conditions along the pond edge created ideal conditions for invasion and likely contributed to the high abundance after only one year. *Typha angustifolia* increased over time in five constructed wetlands in Connecticut (Moore et al. 1999). In a study of a *Typha* invasion in a Lake Michigan coastal wetland, Mitchell et al. (2011) found that *Typha* density (primarily *T. × glauca* and *T. angustifolia*) increased significantly during the first ten years of invasion. Additionally, experiments show that *T. × glauca* can reduce native macrophyte biomass and diversity (e.g., Woo and Zedler 2002; Hall and Zedler 2010; Larkin et al. 2012), and *Typha* litter alone can reduce the abundance and diversity of native plants after only one year (Farrer and Goldberg 2009). In this study, assemblages of one, three, and six species did not provide any short (one year) or longer-term (six years) competitive advantage. Additionally, the competitive dominance of *Typha* spp. does not seem to have been hindered by the native plantings.

Pontederia cordata and *Scirpus* spp. were more abundant outside of the plots in slightly deeper water. In addition, many individuals of *Scirpus* spp. (likely *Bolboschoenus fluviatilis*) were found outside of the plots in shallower water,

closer to the shoreline. Although these two groups of species were not represented in the 2016 plot data, it seems that they were able to coexist with *Typha* spp. at different water depths. The competitive advantage of many emergent species has been shown to vary substantially with subtle changes in water depth (e.g., Olson and Doherty 2012). Whether these species were excluded from other areas due to competition with *Typha* spp. or gradually shifted to more optimal sites is difficult to determine. *Pontederia cordata* can grow well in deeper water compared to most *Typha* spp., (Nichols 1999) and *B. fluviatilis* has been shown to establish under a wide range of water depths (Galatowitsch and van der Valk 1996) but produce the most biomass under shallowly flooded conditions (Hudon 1997). These observations also highlight one of the limitations of *a priori* study designs in dynamic systems. As the system changed over time, species were able to establish outside of our study plots, and that shift was difficult to capture within our predefined study plots. This is not surprising as stormwater retention ponds have been shown to have flashy hydroperiods (Bonilla-Warford and Zedler 2002), and it is difficult to predict such dynamics during the planting phase. Therefore, we recommend that future efforts to establish native plant communities within stormwater retention ponds consider planting native species over a broader range of water depths and planting species adapted to different water depths.

CONCLUSION

Despite the overwhelming invasion by *Typha* spp. shortly after the planting of the native species, all but one of the native species persisted, albeit most of them at low frequency. *Pontederia cordata* and *Scirpus* spp. showed some resistance to invasion, and the cover of *P. cordata*, although low, was stable over six years. This study shows that while *Typha* spp. may readily invade the emergent zone of artificial retention ponds, planting native species during pond creation may increase diversity, even without follow-up management. We recommend the use of *P. cordata* and *Scirpus* spp. as good options to increase native plant richness in stormwater retention ponds.

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GROWTH AND CLIMATE RESPONSE OF FOUR NEW *TSUGA CANADENSIS* (L.) CARRIÈRE (EASTERN HEMLOCK) TREE-RING CHRONOLOGIES FROM MICHIGAN'S UPPER PENINSULA

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ABSTRACT

Availability of high-quality primary ecological datasets like tree-ring growth is critical to the progress of ecological sciences. The International Tree-Ring Databank (ITRDB) is the premier public archive for interannual records of tree-ring growth (i.e., “chronologies”); however, there is currently a dearth of available chronologies that extend into the 21st century. In Michigan, none of the available records for eastern hemlock extends past 1983. Unfortunately, this reduces the availability of these chronologies for study of recent ecological and climatological change or for their integration with new environmental measuring technologies. In this paper, we fill part of this gap for northern Michigan and examine how our datasets can inform long-term studies of ecology-climate interactions in the Midwest region. We present multi-century *Tsuga canadensis* (L.) Carrière (eastern hemlock) tree-ring growth records for four sites in the Upper Peninsula of Michigan, U.S.A., covering the periods 1708–2015, 1754–2015, 1794–2015, and 1857–1995. We explore potential applications of these datasets by examining basic correlations between interannual growth on the one hand and regional temperature and Palmer Drought Severity Index (PDSI, an estimate of dryness) values on the other. At all four sites, growth is negatively correlated with previous summer and current spring temperature, while growth is positively correlated with previous summer PDSI at three of the four sites.

KEYWORDS: eastern hemlock, tree rings, Michigan, Huron Mountains

INTRODUCTION

Insights into past environmental conditions, including climate, are primarily gained through the study of natural proxies. In forested areas, tree rings are one of the most accessible and informative natural proxies available, providing annually resolved information about past environmental variability, such as temperature and precipitation. Public archives that store these proxies for public use, such as the International Tree-Ring Databank (ITRDB), maintained by the US National Oceanic and Atmospheric Administration, provide critical benefits to

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the progress of environmental research (Babst et al. 2017). However, temporal coverage of available tree-ring records (“chronologies”) on the ITRDB is not homogeneous; for instance, nearly half of all chronologies archived have a final ring year preceding 1990 (Larson et al. 2013, Babst et al. 2017). This means that most chronologies do not extend into the 21st century, a period that has witnessed unprecedented shifts in climate (IPCC 2014). This temporal limitation discourages potential integration with newer methods for recording environmental change, such as eddy covariance towers, remote sensing, or phenocams (Babst et al. 2017).

Furthermore, in the Great Lakes region, like many regions in eastern North America, the combined effects of logging, agriculture, and human settlement have removed much of the presettlement forest cover (Gleason 1923, Whitney 1987, White and Mladenoff 1994). Old trees facilitate the construction of multi-century growth records and add intrinsic value to tree-ring studies of the few old-growth forests that still exist in these anthropogenically altered regions. Without information on long-term growth of trees, it is difficult for researchers to assess tree growth patterns over time.

The humid climate of eastern North America prevents extended preservation of dead trees, and old living trees are often the only source of multi-century tree growth information (Fritts 1976). One of the longest-lived tree species in eastern North America is eastern hemlock, *Tsuga canadensis* (L.) Carrière (Cook and Cole 1991). For this reason, it is a preferred species in eastern North America for developing multi-century tree-ring chronologies, and it has been used successfully to assess climate–growth relationships. Often, annual eastern hemlock growth will exhibit a seasonally lagged negative correlation with summer or fall temperature (D’Arrigo et al. 2001, Tardiff et al. 2001, Hart et al. 2010, Saladyga and Maxwell 2015).

However, few new or updated tree-ring chronologies have been made for eastern hemlock in recent years. Of the 76 eastern hemlock chronologies available on the ITRDB, 54 end prior to 1990. Most subsequent published work has focused primarily on the southeastern United States (Hart et al. 2010, Saladyga and Maxwell 2015) or northeastern North America (D’Arrigo et al. 2001, Tardiff et al. 2001, Black and Abrams 2005). In Michigan, all publicly available hemlock chronologies end in 1983 or earlier, thereby creating a critical temporal informational gap that can be filled with strategic data additions and updates to existing data (Larson et al. 2013).

For eastern hemlock, the need to develop high-quality chronologies is even more urgent, since the spread of the invasive *Adelges tsugae* (Annand) (hemlock woolly adelgid) continues to cause hemlock mortality throughout the eastern United States (Hessl and Pederson 2012, Orwig et al. 2012). The northward spread of hemlock woolly adelgid has been slow because it is suspected to be limited by the cooler northern climate (Trotter et al. 2009). However, the range of hemlock woolly adelgid has been expanding further northward as temperatures in North America rise, and it is likely only a matter of time before all hemlocks are affected, including those in northern Michigan (Paradis et al. 2008, Fitzpatrick et al. 2012).

We recognize that there is a need for ecologists to continue to update, de-

velop, and publish quality tree-ring chronologies in order to provide users with the most current and beneficial information available. In regions lacking significant old-growth forest cover, such as eastern North America, multi-century records are essential to extending the temporal scope of analysis available. In this paper, we describe new multi-century tree-ring chronologies at four old-growth eastern hemlock forests in northern Michigan. With each of these datasets, we evaluate their suitability for recording regional climate parameters by comparing interannual ring growth with monthly temperature and Palmer Drought Severity Index (PDSI, a measure of dryness (Palmer 1965)).

METHODS AND MATERIALS

Study sites and sampling procedure

The Huron Mountain Club (HMC) is a privately managed area covering 8,100 ha along the southern coast of Lake Superior in Michigan's Upper Peninsula, approximately 50 km northwest of the city of Marquette. Founded in 1889 as a private retreat, HMC encompasses forests that have largely escaped major logging operations, resulting in the preservation of some of the largest tracts of old-growth forest in the eastern United States. The growing season is typically less than 120 days per year (Sommers 1977).

We sampled three sites at HMC, which we have designated HMC-West, HMC-Rush Lake, and HMC-Mountain Lake (Figure 1). In summer 2016, we collected increment cores at HMC-West and HMC-Rush Lake as part of a project reconstructing biomass dynamics over the last four decades (Dye 2018). However, we have not yet published long-term chronology development and climate response. At both sites, we cored all trees within two 16-m radius plots with diameter at breast height (DBH, approximately 1.3 m above ground) greater than 10 cm. We also incorporated unpublished tree-ring data sampled at HMC-Mountain Lake in 1995. Because HMC-Mountain Lake was sampled 23 years ago, we cannot infer information on recent tree-ring growth as we can at the other sites. Despite this shortcoming, we include it primarily for its contribution to eastern hemlock chronology construction in the region.

Dukes Research Natural Area (Dukes RNA) lies within the Munising Ranger District of the Hiawatha National Forest approximately 40 km inland from Lake Superior (Figure 1). Established in 1979 as a protected research area by the US Forest Service, Dukes RNA harbors stands of old growth hemlock-northern hardwood forests that have escaped significant logging activity. Trees at Dukes RNA were cored in 2016 and have not yet been published. At Dukes RNA, we cored two radii from 30 eastern hemlock trees > 20 cm DBH. All Dukes RNA and HMC trees were synchronized with long-term remeasurement plots to maximize the applicability of the dataset (Woods 2007; Woods 2014).

Tree-ring chronology development

We mounted and sanded each increment core using progressively finer grit sandpaper and confirmed annual dating of each ring through crossdating (Stokes and Smiley 1968). We measured all annual ring widths at 0.001 mm precision with a sliding stage micrometer (Velmex Inc., Bloomfield, NY, USA). Measurements were then verified statistically for crossdating accuracy using the software COFECHA (Holmes 1983). To compile our final site chronologies, we omitted ring width series with segment lengths less than 75 years and correlations with the master chronology of less than 0.32 to avoid bias in the climate growth relationships (Fritts 1976). For each ring-width chronology, we are primarily interested in two statistical characteristics: interseries correlation and mean sensitivity. The interseries correlation is the average of all correlations calculated between each individual series and the remaining series upon removal of the series being tested (Holmes 1983). Average mean sensitivity quantifies relative differences between consecutive growth rings, serving as an indicator of growth sensitivity to environmental conditions (Fritts 1976). Both of these measures are useful for comparing characteristics of the chronologies presented here with other chronologies.

To remove non-climatic growth responses such as release events and age-related growth trends (Cook and Peters 1981), we detrended and standardized each raw ring width series using a 30-year

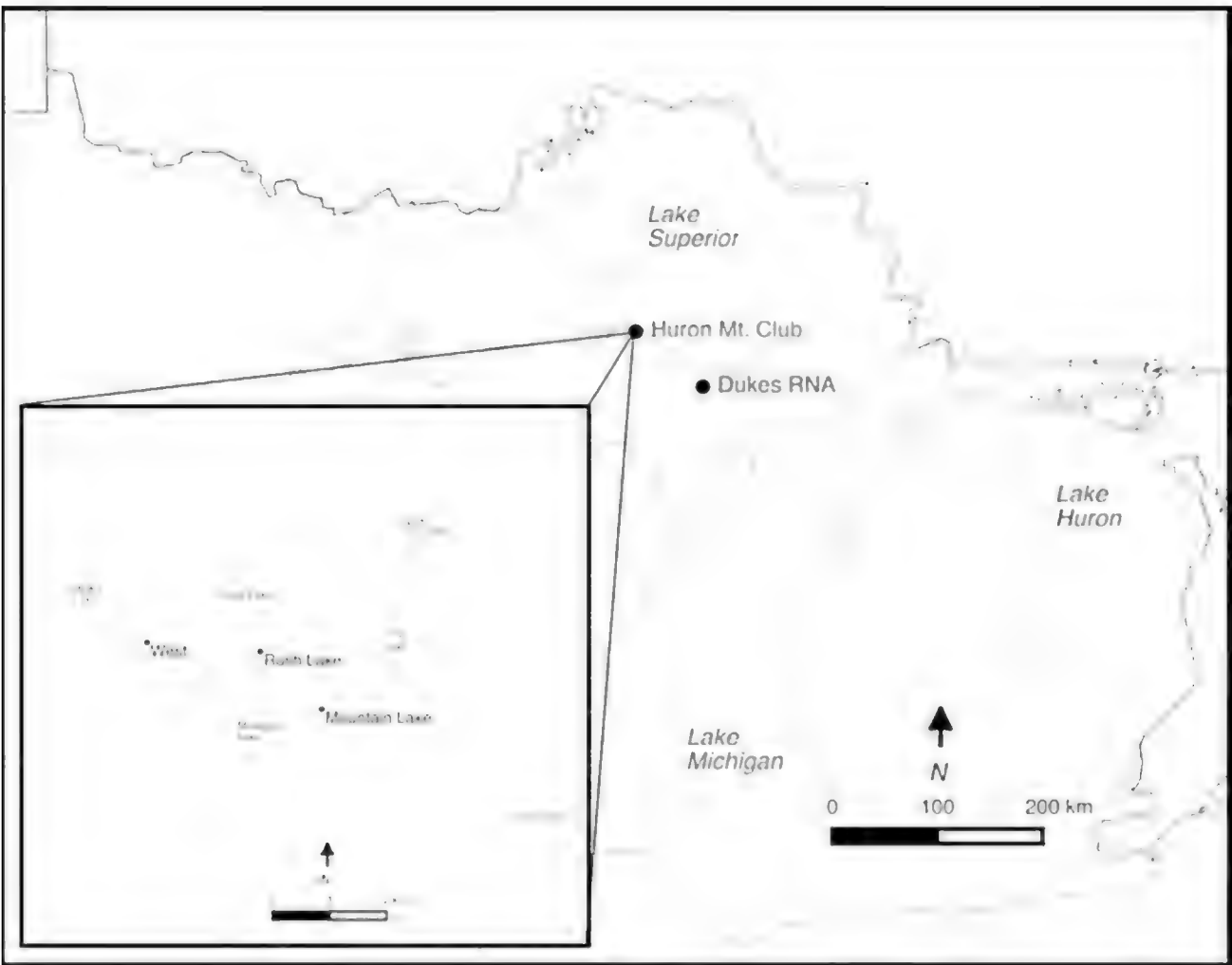


FIGURE 1. Map showing the location of the study sites. The Huron Mountain Club area is expanded in an inset for detail. Map layout was created with QGIS Version 2.8.2 (QGIS, 2015). Basemap layers consist of U.S. state border lines (U.S. Census Bureau, 2017a), local lake boundaries (U.S. Census Bureau 2017b), and Canadian national borders (Statistics Canada, 2016).

smoothing spline in the R package dplR (Bunn 2008). The 30-year spline has been used as an effective detrending technique in eastern hemlocks (Hart et al. 2010, Saladyga and Maxwell 2015). Although tree-ring widths are often autocorrelated with past growth, we opted not to remove this autocorrelation to enable comparisons with previous year climate. Each year of all detrended series per site were then averaged to create a single mean chronology time series for each site. We constructed chronologies only for years when there were at least five individual samples.

Climate-growth relationships

We compare each of our four detrended tree-ring chronologies with monthly mean temperature and monthly Palmer Drought Severity Index (PDSI). Instrumental records for each of these variables were downloaded for the years 1895–2015 from the National Climate Data Center Michigan climate division 1 (National Oceanic and Atmospheric Administration 2016). Divisional climate data tends to be more strongly related to tree growth than do single stations (Blasing et al. 1981). In particular, NCDC divisional data has successfully been used in several dendroclimatological studies in the eastern U.S. (Hart et al. 2010, Maxwell et al. 2015, Saladyga and Maxwell 2015).

We conducted correlation analyses between each tree-ring chronology and monthly temperature and PDSI, from previous-year June to current-year September. Because we correlate growth with previous year climate, we begin climate-growth comparisons in 1896. All correlation analyses were conducted in the R package treeclim (Zang and Biondi 2016). Package treeclim conducts Pearson product moment correlation coefficients between the chronology and monthly climate, constructing confidence intervals and statistical significance based on partial regression coefficients from 1000 bootstrapped estimates ($\alpha < 0.05$).

For each monthly climate variable that returned a significant growth-climate relationship, we additionally produced separate correlation coefficients for the pre-1983 period (1895–1983), the post-1983 period (1983–2015) period, and the full period (1895–2015) at Dukes RNA, HMC-Rush Lake, and HMC-West. We did not produce separate correlations for HMC-Mountain Lake because this chronology ends in 1995. Because there are no eastern hemlock chronologies publicly available on the ITRDB for Michigan that extend past 1983, this shows whether there has been an observable change in the climate-growth relationships for Michigan hemlocks since the period when most hemlock chronologies end.

RESULTS

Tree-ring chronologies

Each chronology strongly crossdates internally and has interseries correlations confirming confident crossdating that are consistent with other publicly available eastern hemlock tree-ring chronologies (Table 1; Figure 2). Mean sensitivity, an indicator of interannual variation in tree growth, is high for each chronology. The average mean sensitivity of eastern hemlock chronologies archived on the ITRDB is 0.24 (maximum = 0.34 and minimum = 0.19; Hart et al. 2012). Consequently, mean sensitivity for each of our chronologies is towards the upper limit of what is typical for eastern hemlock.

Climate-tree growth relationships

Tree growth at all four sites is significantly negatively correlated with temperature for one or more months in the previous summer and significantly positively correlated with one or more months in the current spring (Figure 3). Growth at HMC-Rush Lake is correlated with temperature for each of previous June-October, HMC-West and Dukes RNA are correlated with previous June-September, and HMC-Mountain Lake is correlated only with previous August. Current-year March and/or April temperature is positively correlated with growth at all sites.

PDSI is positively correlated with growth for all months except current-year August and September at HMC-West. Previous summer PDSI is positively correlated with growth at Dukes RNA (previous June-November) and HMC-Rush

TABLE 1. Statistics for each of the four tree-ring chronologies.

Site	Number of trees sampled	Dated radii	Time span	Average interseries correlation	Average mean sensitivity
Dukes RNA	25	39	1693–2015	0.692	0.257
HMC-Rush Lake	53	86	1747–2015	0.690	0.336
HMC-West	77	140	1777–2015	0.687	0.326
HMC-Mountain Lake	37	43	1836–1995	0.544	0.386

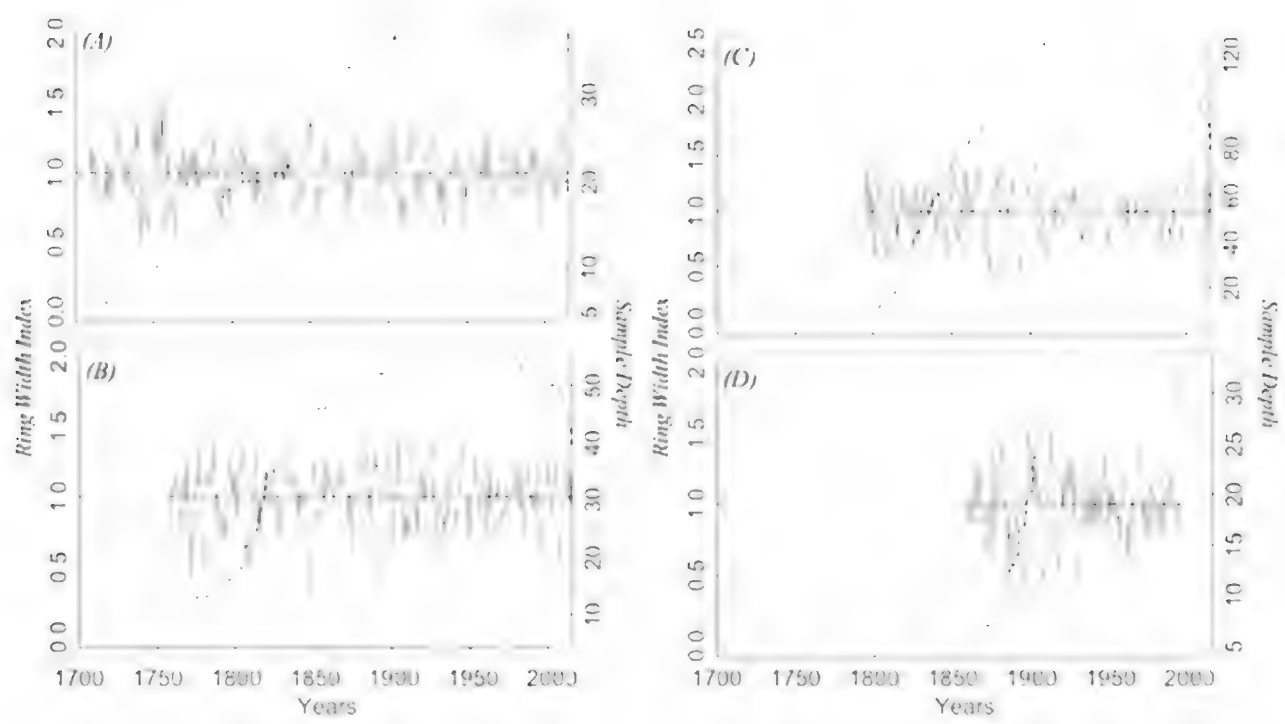


FIGURE 2. Detrended, standardized ring width indices (left axis) with sample depth (right axis) for (A) Dukes RNA; (B) HMC-Rush Lake; (C) HMC-West; and (D) HMC-Mountain Lake. The solid black line denotes the average chronology, and light gray shaded regions indicate 95% confidence intervals around the mean.

Lake (previous August and November). In contrast, growth at HMC Mountain Lake is negatively correlated with PDSI in previous year June.

At some sites, the climate-growth relationship differs between the pre- and post-1983 periods (Table 2). At Dukes RNA, monthly temperature and PDSI relationships are consistently much less correlated with growth in the pre-1983 period; for temperature, the sign changes from negative (pre-1983) to positive (post-1983) during all months. Changes in correlations are less consistent at HMC-Rush Lake and HMC-West. At these sites, correlations become stronger with some monthly climate variables but become weaker with others (Table 2).

DISCUSSION

Climate-growth relationships of hemlock chronologies

In the eastern U.S., studies relating tree growth and climate have a robust history for eastern hemlock (D’Arrigo et al. 2001, Black and Abrams 2005, Hart et al. 2010, Saladyga and Maxwell 2015). Typically, hemlock is one of the oldest-lived trees in the eastern U.S. and can exceed 500 years old (Cook and Cole 1991), making it a primary target for development of long term tree-ring archives. In other dendroclimatological analyses, eastern hemlock growth is often negatively correlated with previous summer temperatures (D’Arrigo et al. 2001, Tardiff et al. 2001, Hart et al. 2010, Saladyga and Maxwell 2015). Likewise, this is the case with each of our four chronologies (Figure 3). Potentially,

TABLE 2. Monthly correlation coefficients for temperature and for Palmer Drought Severity Index (PDSI) for the pre-1983 period (1895–1983), the post-1983 period (1983–2015) period, and the full period (1895–2015) at Dukes RNA, HMC-Rush Lake, and HMC-West. Correlations for HMC-Mountain Lake are not shown because this chronology ends in 1995. Only those monthly climate variables that were deemed significant are included. Previous-year months are listed with a lowercase “p” preceding the name of the month; for example, previous-year June is listed as “pJun.”

Month	Dukes RNA			HMC-Rush Lake			HMC-West		
	Pre-1983	Post-1983	Full	Pre-1983	Post-1983	Full	Pre-1983	Post-1983	Full
<i>Temperature</i>									
pJun	−0.28	0.04	−0.32				−0.33	−0.52	−0.38
pJul	−0.36	0.16	−0.38	−0.15	−0.28	−0.21	−0.27	−0.43	−0.35
pAug	−0.28	0.19	−0.32	−0.37	−0.40	−0.36	−0.30	−0.44	−0.34
pSept	−0.30	0.16	−0.29	−0.34	−0.25	−0.31	−0.33	−0.10	−0.26
pOct				−0.21	−0.12	−0.20	−0.33	−0.52	−0.38
pNov									
pDec									
Mar	0.24	0.15	0.24	0.31	0.21	0.27	0.30	0.10	0.20
<i>PDSI</i>									
pJun	0.24	−0.08	0.16				0.20	0.21	0.21
pJul	0.35	0.05	0.26				0.37	0.33	0.35
pAug	0.32	0.13	0.27	−0.08	0.20	0.19	0.38	0.38	0.37
pSept	0.29	0.15	0.25				0.36	0.37	0.36
pOct	0.25	0.02	0.19				0.39	0.24	0.33
pNov	0.27	0.01	0.19	−0.01	0.07	0.18	0.38	0.22	0.32
pDec							0.34	0.23	0.29
Jan							0.31	0.26	0.28
Feb							0.32	0.22	0.28
Mar							0.31	0.15	0.25
Apr							0.24	0.12	0.18
May							0.28	0.20	0.24
Jun							0.40	0.19	0.32
Jul							0.34	0.13	0.26

this is related to a delayed negative effect of high temperatures—that is, warmer temperatures accelerate evapotranspiration, increasing water loss and environmental stress on the tree (Cook and Cole 1991). This effect can be particularly drastic for eastern hemlock, since the desired temperature range of the species is small and photosynthesis noticeably begins to decline after temperatures crest this threshold (Adams and Loucks 1971). Additionally, tree growth is positively correlated with current-year spring temperatures in at least one month (March and/or April) at all sites. Most likely, this is a response to longer growing season length. Warmer spring months induce an earlier start to the growing season, which facilitates enhanced tree growth over the course of that year (D’Arrigo et al. 2001).

Growth correlations with PDSI vary more strongly between sites (Figure 4). HMC West exhibits high positive correlations with PDSI in all months except

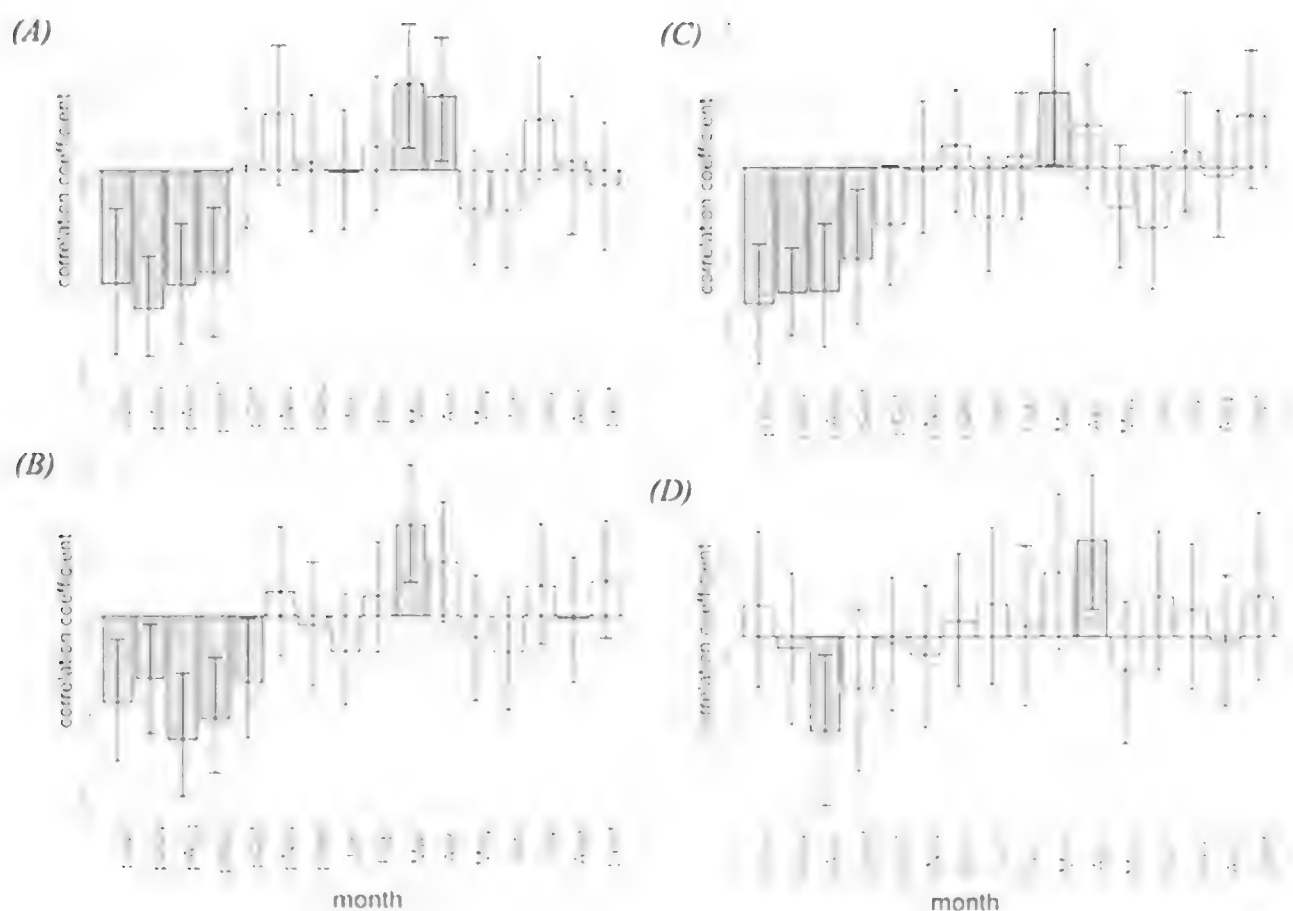


FIGURE 3. Correlations between average monthly temperatures and tree-ring chronologies at (A) Dukes RNA; (B) HMC-Rush Lake; (C) HMC-West; and (D) HMC-Mountain Lake. Correlation values are shown by the heights of the bar plots, with significantly correlated months shaded in gray. Vertical solid black lines indicate 95% confidence intervals for the monthly correlations.

current-year August and September. This likely reflects drier site characteristics. However, HMC-West also has many more samples ($n = 75$) than the other sites, potentially biasing the monthly PDSI correlations. In contrast, HMC-Rush Lake and Dukes RNA respond positively only to previous summer PDSI and weakly correlate with current-year PDSI. Growth is negatively correlated with previous June PDSI at HMC-Mountain Lake. Differences in climate response here may be related to either microsite climate differences due to its position on the northeast corner one of the larger lakes at HMC (Hinkel and Nelson 2012) or the lack of ring width measurements from 1995 to present. The Mountain Lake chronology also has both the highest mean sensitivity (0.391) and lowest interseries correlation (0.549), which could potentially be reflective of the anomalously negative June PDSI relationship.

Tree-ring chronologies of other species in Michigan and the surrounding region exhibit climate-growth relationships similar to those we observed for eastern hemlock. In the Lower Peninsula of Michigan, red pine (*Pinus resinosa* Aiton) biomass growth is negatively correlated with previous spring temperature and positively correlated with a current-summer drought index (Magruder et al. 2012). Sugar maple (*Acer saccharum* Marshall), balsam fir (*Abies balsamea* (L.) Mill.), and white spruce (*Picea glauca* (Moench) Voss) north of Lake Superior in southern Ontario are negatively correlated with previous spring temperature, although the current-year spring temperature relationship emerges only in balsam

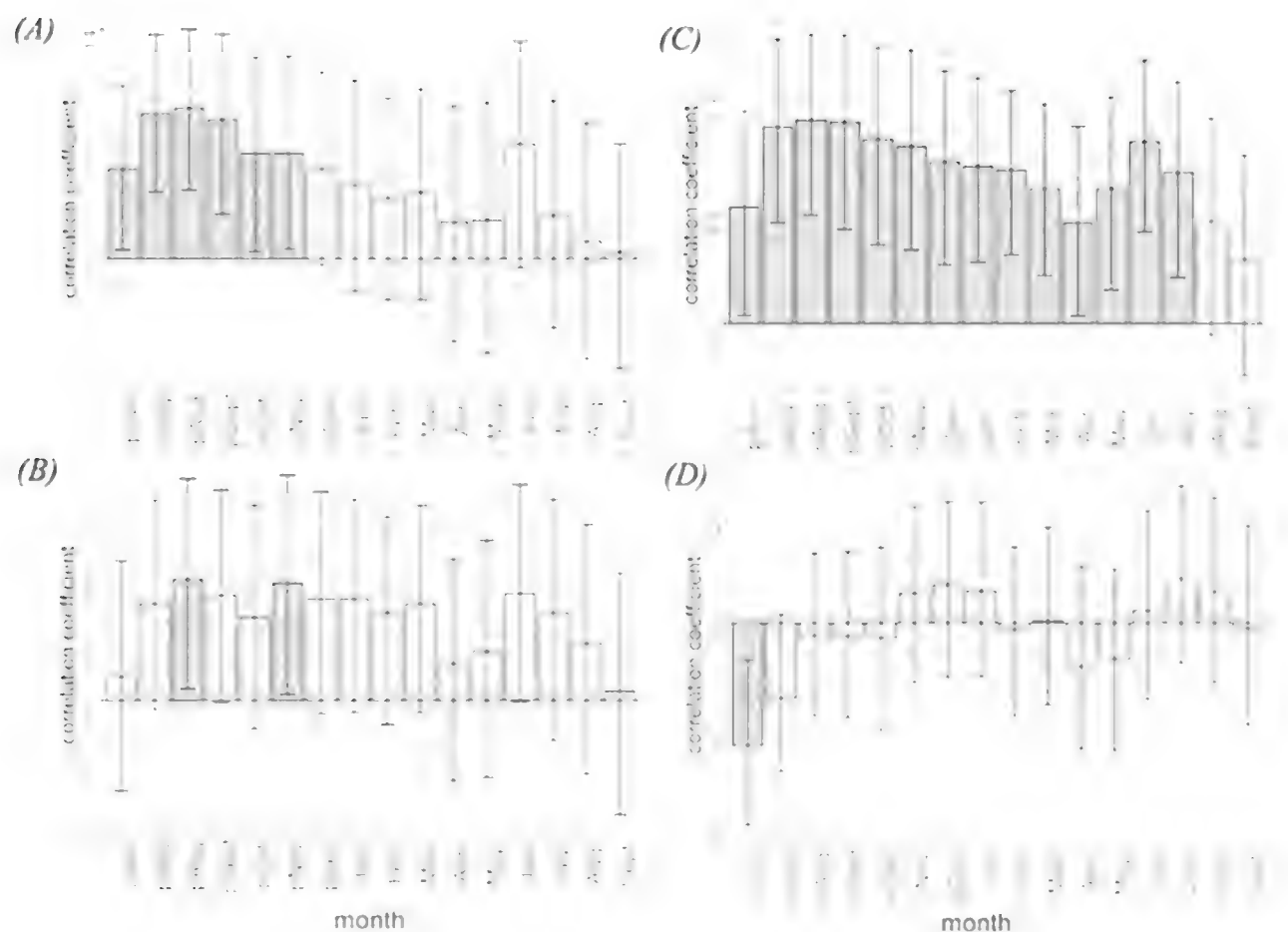


FIGURE 4. Correlations between monthly PDSI and tree-ring chronologies at (A) Dukes RNA; (B) HMC-Rush Lake; (C) HMC-West; and (D) HMC-Mountain Lake. Correlation values are shown by the heights of the bar plots, with significantly correlated months shaded in gray. Vertical solid black lines indicate 95% confidence intervals for the monthly correlations.

fir (Goldblum and Rigg 2005). Across an Upper Midwest longitudinal gradient, sugar maple growth is negatively correlated with previous spring temperature (Lane et al. 1993); and, in Quebec, American beech (*Fagus grandifolia* Ehrh.) and sugar maple are both negatively correlated with previous summer temperature (Tardiff et al. 2001).

Utility of the dataset

The primary goal of this paper is to construct four high-quality old-growth eastern hemlock tree-ring chronologies and make them available for use on a public archive, thereby accelerating environmental and earth science research (Babst et al. 2017). Although the spatial and temporal coverage of the ITRDB has grown to include over 4000 sites on six continents, many of the currently archived chronologies were submitted prior to 1990 and lack information on recent growth (Larson et al. 2013). For eastern hemlock alone, only 24 of the 76 available chronologies available for North America extend past the year 1990. In Upper Peninsula Michigan specifically, our chronologies are currently the only publicly available eastern hemlock chronologies that extend past 1983. We extend the temporal data availability for this region by 12 years at HMC-Mountain Lake and by 33 years at HMC-Rush Lake, HMC-West, and Dukes RNA. In a re-

gion containing some of the largest tracts of old-growth hemlock forest in North America, extending and updating available growth records is essential (Hessl and Pederson 2012). Few other sources exist to study long-term tree growth in Michigan or in eastern deciduous forests in general besides utilizing the current old-growth trees (but see De Graauw (2017) and Rochner et al. (2017) for recent work on using logs from historic structures, although these lack information on current tree characteristics).

The location of our chronologies within two active research forests also amplifies their utility for a variety of environmental research. Current parallel datasets include dendroecology of red pine (Guyette et al. 2012) and white pine (*Pinus strobus* L.) (Fahey and Lorimer 2014), fine-scale climate monitoring (Hinkel and Nelson 2012), biomass dynamics (Woods 2014, Dye 2018) at HMC, and maintenance of long-term monitoring plots of growth and mortality (Woods 2007, Woods 2014) and LiDAR measurements (Fahey et al. 2015) at both HMC and Dukes RNA. Aggregation of ancillary co-located datasets such as these can be instrumental to improving scientific understanding of ecosystem processes and variability in the face of changing climate (Babst et al. 2017, Haase et al. 2018), but only if scientists take the time to publish, share, and archive their datasets.

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THE ALLELOPATHIC EFFECT OF *RHAMNUS CATHARTICA* L. LEAVES AND FRUIT

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ABSTRACT

The purpose of this study was to examine changes in the allelopathic effect of *Rhamnus cathartica* L. (Common or European buckthorn) based on its stage in the yearly growth of new leaves and the distribution of allelopathic properties in different parts of the plant by creating solutions of *R. cathartica* leaves and fruit in various concentrations and applying them to radish seeds. Unsuccessful germinations of the radish seeds (to which old leaf solutions, new leaf solutions, and fruit solutions were applied) were counted, and thus, their allelopathic effects were compared. Convincing evidence of unevenly distributed allelopathic properties in *R. cathartica* which vary based on the stage of growth (new leaves versus old leaves) was found. Both the new leaves and the fruit showed allelopathy while older leaves showed little or no allelopathic effects.

INTRODUCTION

Rhamnus cathartica L. is a deciduous shrub or small tree which ordinarily reaches from sixteen to twenty-five feet in height. Plants can be either male or female, but both sexes have elliptical to oval, mainly subopposite, glabrous green leaves that turn yellow in the fall (Missouri Botanical Garden 2016). *Rhamnus cathartica* is classified in Wisconsin as a Restricted Invasive, which indicates that *R. cathartica* plants “cause or have the potential to cause significant environmental or economic harm or harm to human health” (Wisconsin Department of Natural Resources 2018). Although in certain environments *R. cathartica* establishment is improbable (Gill and Marks 1991), in Wisconsin, *R. cathartica* is quite common (Seltzner and Eddy 2003). There are a few different reasons why *R. cathartica* has been given the classification of a Restricted Invasive. However, the two prominent reasons given by the Wisconsin Department of Natural Resources for this classification are coverage/shading, whereby *R. cathartica* retards the germination and growth of understory species, and allelopathy.

Allelopathy is the ability of certain plant species to inhibit the growth of other plants in their surroundings through the release of secondary chemicals. The inhibition of growth of surrounding plants can further lead to rapid expansion of

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the allelopathic plant given ideal circumstances (e.g., sufficient sunlight, water, nutrients). For this reason, the great majority of non-native allelopathic plants are considered invasive. Past research has indicated the presence of allelopathic chemicals in *R. cathartica*, including anthraquinones, tannins, and flavonoids, of which emodin (an anthraquinone) is by far the most abundant (Warren et al. 2017). However, other research seems to suggest that *R. cathartica* does not have an advantage in ecosystems because of allelopathy, but rather, due only to its dense coverage and early germination season (Zumwalde n.d.). There are also indications that season has an effect on the allelopathic action of some plants, possibly including *R. cathartica* (Izhaki 2002). It is important to note that different studies of allelopathy using different parts of the *R. cathartica* (fruit, leaves, bark, roots) have found inconsistent results. For example, Seltzner and Eddy (2003) found that alfalfa seed germination dropped when treated with the drupes, but not when treated with the leaves, bark, or roots. Warren et al. (2017) on the other hand found that a mixture of *Rhamnus cathartica* leaf and root treatments decreased Mesocosm species' richness and abundance. Izhaki (2002) suggested that the presence and distribution of emodin, a major secondary metabolite with possible allelopathic effects, might be dependent on season and light intensity.

This leads us to believe that different parts of *Rhamnus cathartica* plants contain different amounts or different types of allelopathic chemicals. As noted above, there is also reason to believe that season has an effect on the allelopathic properties of *R. cathartica*. Accordingly, we hypothesize that (1) at least one batch of solutions (old leaves, new leaves, or fruit) will show allelopathic properties; (2) the fruits of *R. cathartica* will have a different allelopathic strength than the leaves of *R. cathartica* on the germination of radish (*Raphanus raphanistrum* L.) seeds; and (3) old leaves (already fallen leaves) of *R. cathartica* will have a different allelopathic strength than new leaves (just on trees) on the germination of radish seeds.

METHODS AND MATERIALS

In this study, the difference between the allelopathic effect on the germination of radish seeds of *Rhamnus cathartica* leaf and fruit solutions from different seasons was examined. All the leaves and fruits of *R. cathartica* used in this study were collected randomly from five sites on a property in Green Lake, Wisconsin. These sites contained varying densities of *R. cathartica*, ranging from one shrub per 25 m² to 47 shrubs per square meter. The sites used also contained a variety of ages of *R. cathartica* as apparent in their sizes from twenty centimeters in height to about five meters in height. Fruits and new leaves were taken directly from the shrubs, whereas old leaves, those that had fallen from the shrubs, were collected from just beneath the shrubs. Old leaves were collected in mid to late April, as were the fruits after they had overwintered, and new leaves were collected in early May. Because this research, which was a class project, took place during the Spring semester, we were unable to collect fresh fruits for this study before the end of the semester in late May. To create the solutions, 80 grams of the leaves or fruit were mashed in a blender and mixed with 800 ml of distilled water. These solutions were then strained to remove all large particles of fruit and leaves. The resulting concentrated solution was considered the 100% solution and diluted using distilled water to create the lower concentration solutions of 0.001%, 0.01%, 0.1%, 1%, 5%, 10%, 25%, 50%, and 75% based on the 100% concentrated solution. Distilled water (0% solutions) was used for the control in each batch. These solutions were refrigerated between watering to avoid changes in concentration or the catalyzing of any natural processes (e.g., fermentation).

It was decided to use radish seeds because of their fast germination rate, availability, and low cost. Petri dishes were prepared by placing cut filter paper in them and spreading out 15 radish seeds in each petri dish (with petri dish covers). Two petri dishes were used for each concentration of each batch. These petri dishes were placed in an environment with a medium amount of sunlight and retained their covers for the entirety of the experiments. These petri dishes were treated with the *R. cathartica* solutions every other day with enough solution to saturate the filter paper (ca. 3–4 ml). Photos were taken of the lab setup after each week of growth. The photographs were used as a backup counting method. The radishes grew over a span of two weeks, after which the number of successful and unsuccessful germinations were recorded using the photos to confirm the counts. When a difference occurred between the photograph and the in-person counts, the in-person counts were used. The data was analyzed in two ways: First, using a chi-squared (χ^2) test for homogeneity with 10 degrees of freedom for each batch of solutions (old leaves, new leaves, and fruit) and second, by graphing the percentage concentration of the solution versus the proportion of unsuccessful germinations. The null hypothesis is that all concentrations result in the same proportion of unsuccessful seed germinations, and the alternative hypothesis is that at least one concentration results in a different proportion of seed unsuccessful germinations. Each chi-squared test was analyzed using a significance level $\alpha=0.05$. Regressions of the data from all three trials were analyzed using Logger Pro. A linear fit was used to analyze data from the old leaves, while the data from both the new leaves and the fruit were analyzed using an automatic fit.

RESULTS

Table 1 summarizes the observed counts from the radishes watered with the solutions of the old leaves. The chi-squared test for the old leaves resulted in a χ^2 value of 10.615 ($p = 0.388$). Because $p>\alpha$ ($0.388>0.05$), we fail to reject the null hypothesis and conclude that there is not convincing evidence that any concentration of the old leaf solution produced a different amount of successful seed germination versus amount of non-successful seed germination than other concentrations of the old leaf solution.

Table 2 summarizes the observed counts from the radishes watered with the solutions of the new leaves. The chi-squared test for the new leaves resulted in a χ^2 value of 146.352 ($p = 2.10 \times 10^{-26}$). Because $p<\alpha$ ($2.10 \times 10^{-26}<0.05$), we reject the null hypothesis and conclude that there is convincing evidence that at least one concentration of the new leaf solution produced a different proportion of successful seed germination than the other concentrations of the new leaf solution.

Table 3 summarizes the observed counts from the radishes watered with the

TABLE 1. Radish seed germination counts for old leaf solutions.

	Concentration of Solution										
	0%	0.001%	0.01%	0.1%	1%	5%	10%	25%	50%	75%	100%
Number of Successful Germinations	29	27	28	25	26	29	27	29	25	28	29
Number of Unsuccessful Germinations	1	3	2	5	4	1	3	1	5	2	1

TABLE 2. Radish seed germination counts for new leaf solutions.

	Concentration of Solution										
	0%	0.001%	0.01%	0.1%	1%	5%	10%	25%	50%	75%	100%
Number of Successful Germinations	29	29	28	26	27	26	28	25	29	19	1
Number of Unsuccessful Germinations	1	1	2	4	3	4	2	5	1	11	29

TABLE 3. Radish seed germination counts for old fruit solutions.

	Concentration of Solution										
	0%	0.001%	0.01%	0.1%	1%	5%	10%	25%	50%	75%	100%
Number of Successful Germinations	28	29	26	28	26	27	27	29	21	7	2
Number of Unsuccessful Germinations	2	1	4	2	4	3	3	1	9	23	28

solutions of the fruit. The chi-squared test for the fruit resulted in a χ^2 value of 158.301 ($p = 7.26 \times 10^{-29}$). Because $p < \alpha$ ($7.26 \times 10^{-29} < 0.05$), we reject the null hypothesis and conclude that there is convincing evidence that at least one concentration of the fruit solution produced a different proportion of successful seed germination than the other concentrations of the fruit solution.

Figure 1 is a graph of the percentage of concentrated solution versus the proportion of unsuccessful germinations. The data for Figure 1 was analyzed using Google Sheets. The standard deviation for the old leaves was lower at 0.0524 than for the new leaves and the fruit, which were higher at 0.275 and 0.311, respectively. The slope of the linear fit for the old leaves was approximately zero and has a correlation of 0.2035. The automatic fit for both new leaves and fruit used quadratic regressions and found a correlation of 0.9644 for the new leaves and 0.9730 for the fruit. Figure 1 is aggregated so that values for lower concentration are more visible.

DISCUSSION

The p-values from the chi-squared tests for both new leaves and fruit were highly significant while the old fruits showed no significant effects on seed germination. Based on the regressions, the new leaves and the fruit show clear relationships between concentration of solution and proportion of germinations while the regression of the old leaves indicates the lack of a relationship between

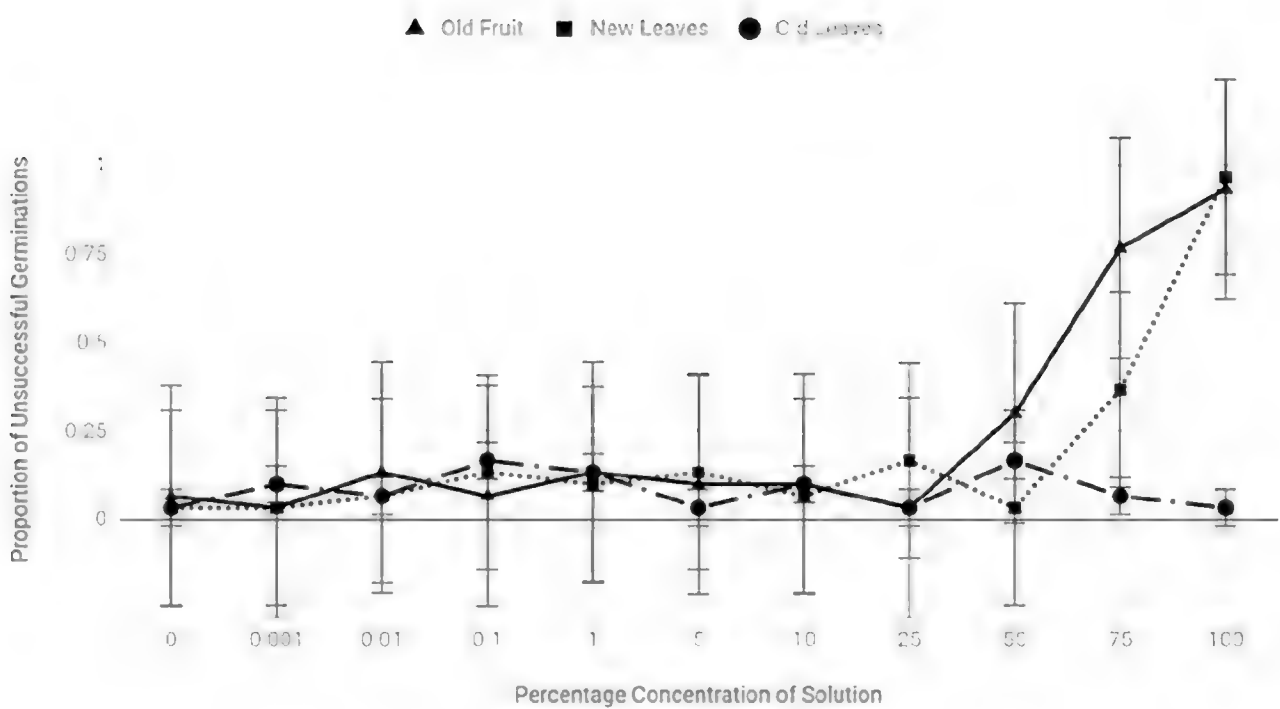


FIGURE 1. The effect of various concentrations of solutions of new leaves, old leaves, and fruits of *Rhamnus cathartica* on germination of radish (*Raphanus raphanistrum*) seeds. Error bars indicate one standard deviation.

concentration of solution and proportion of germinations. This shows evidence of allelopathic properties in both the new leaves and the fruit.

Because error is calculated using standard deviation or the overall spread of the data, the errors for new leaves and fruit were higher. Error values less than zero or greater than one are negligible because it would be impossible to have a negative number of unsuccessful germinations or to have more than thirty seeds with unsuccessful germination when only thirty seeds were tested.

Thus, there is convincing evidence in favor of part one of our hypothesis, that at least one batch of the solutions made from *Rhamnus cathartica* exhibits allelopathic properties. Part two of our hypothesis, that there is a significant difference between the allelopathic effect of the fruit and that of the leaves is indicated by the chi-squared tests, because old leaves showed no significance while fruit did show significance. In this case, the fruit exhibits a greater allelopathic effect than the leaves. Part three of our hypothesis, that over time (about one year), the allelopathic effect of *R. cathartica* will change. In this case, Figure 1 shows convincing evidence of a relationship between concentration of new leaf solutions and the proportion of germination but no significant relationship is shown for old leaf solutions. Thus, it appears that the old leaves showed a decrease in allelopathic properties from the time at which the leaves sprouted in the spring of 2018 to the time they were collected in April 2019.

There may be some error based on the way in which the old leaves were collected. Because these leaves were collected from the ground beneath the tree instead of from the tree itself, they may have been subjected to increased water flow in the fall after they had fallen and in the spring during the melting season. Since water was used in this experiment, it was shown that some, if not most, of

the allelopathic chemicals in *R. cathartica* can be transferred by water. Thus, water flow could have transported some of the allelopathic chemicals of *R. cathartica* into the ground before the leaves were collected. Also, because leaves were littered on the ground, it is possible that an occasional leaf or stem from a different species might have been mixed into this batch. Nevertheless, the results of this study follow the conclusion of Warren et al. (2017) and other studies that there seem to be allelopathic mechanisms at play in *R. cathartica*.

CONCLUSION

All three parts of our hypothesis are supported by the results of this study. Through this study evidence was shown of an unevenly distributed allelopathic effect which varies through different parts of the flowering process. More research on the differences between new and old fruit may be warranted. For the purpose of this experiment, it was not possible to sample new fruits in order to test their allelopathic results. Some studies exist which examine all parts of *R. cathartica* for allelopathic effect (leaves, fruit, bark, and roots), but additional experiments are needed which compare all parts at once. It should also be noted that while extensive research is available on the distribution of allelopathic chemicals in *R. cathartica*, little of it examines the changes in allelopathic chemicals of *R. cathartica* as the plant ages. The importance of this study is apparent in that the allelopathic chemicals of plants such as *R. cathartica* may provide a natural alternative to glyphosate-based herbicides such as Roundup®. These herbicides have been subject to controversy in recent years, after the World Health Organization (2016) determined glyphosate and two other less common pesticide ingredients to be “‘probably carcinogenic’ to humans.”

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BRYOPHYTES OF ST. MARTIN ISLAND, DELTA COUNTY, MICHIGAN

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ABSTRACT

The first bryological survey of St. Martin Island, Delta County, Michigan was conducted in 2013 and 2014; it is only the second bryological survey of any island in the Grand Traverse Islands archipelago in northwestern Lake Michigan. The island has an area of 523 ha, is located 15 km south of the tip of the Garden Peninsula, and is underlain by Niagara dolomite, which outcrops as cliffs, particularly on the west coast. The predominant vegetation type is hardwood and mixed conifer-hardwood forests, and there is a small ephemeral pond and hardwood swamp in the northern part of the island. A total of 105 species of bryophytes (81 mosses and 24 liverworts) were recorded from St. Martin Island. Its bryophyte diversity is comparable to that of nearby Summer Island. Thirty species of mosses and ten species of liverworts represent new records for Delta County.

KEYWORDS: St. Martin Island, Delta County, Michigan, Lake Michigan islands, bryophytes

INTRODUCTION

St. Martin Island (45°30' N, 86°46' W) has an area of 523 ha and is situated in northwestern Lake Michigan in Delta County, Michigan. It is part of the Grand Traverse Islands archipelago (Judziewicz 2001, Judziewicz et al. 2016) and is located approximately midway between the southern tip of the Garden Peninsula (in Michigan) to the north, and the northern tip of the Door Peninsula (Wisconsin) to the south. Underlain by Niagara dolomite that outcrops as cliffs up to 25 meters tall on the western coast, the majority of the island is dominated by second-growth forests (Figure 1) of sugar maple (*Acer saccharum* Marshall), beech (*Fagus grandifolia* Ehrh.), yellow birch (*Betula alleghaniensis* Britton), and red oak (*Quercus rubra* L.), with white cedar (*Thuja occidentalis* L.) and balsam-fir (*Abies balsamea* (L.) Mill.) more frequent near the coasts, especially on cliffs. There is a small four-hectare ephemeral pond and adjacent hardwood swamp (centered at 45°30'12" N, 86°45'43" W), which

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FIGURE 1. Mixed hardwood–conifer forest on the trans-island trail a short distance north of the center of the island, July 16, 2013. The persons on the trail are US Fish & Wildlife Service Biologist Sadie O’Dell, Karsten Crouse, and Virginia Freire. Photo by Emmet J. Judziewicz.

is dominated by green ash (*Fraxinus pennsylvanica* Marshall), present near the lighthouse in the northeastern part of the island that has a very diverse bryophyte flora. A recent, more detailed discussion of the island’s geography, plant communities, and vascular flora can be found in Judziewicz et al. (2016). Except for a few small inholdings, since 2015 St. Martin Island is now part of the Green Bay National Wildlife Refuge and is administered by the U.S. Fish & Wildlife Service.

MATERIALS AND METHODS

A total of five days of fieldwork were conducted on July 16–17, 2013 (by Freire alone) and on August 18–20, 2014 (by Freire and Route); Judziewicz also participated in this field work during both visits, collecting vascular plants, and a few bryophytes.

Areas collected included the southern part of the steep west coast bluffs; the entire main trans-island trail from the old fishing village in the south to the lighthouse in the north; secondary trails running east and west from this main trail; smaller interior outcrops in the south, east of the village; bare, horizontal dolomite bedrock fronting Lake Michigan; and the wetlands surrounding the ephemeral pond/wetland in the northeast a short distance inland from the lighthouse. The specimens collected are deposited in the Robert W. Freckmann Herbarium (UWSP) at the University of Wisconsin-Stevens Point in Stevens Point, Wisconsin. Most specimens were identified using Crum (1991, 2004) and, in a few instances, Flora of North America Editorial Committee (2007, 2014).

RESULTS

A total of 233 bryophyte specimens were collected, and they represent 81 species of mosses and 24 species of liverworts, for a total of 105 bryophyte species, which are listed below. Each entry consists of the name of the species and the collection number. If the species is new to Delta County, Michigan (according to the Consortium of North American Bryophyte Herbaria, 2020), it is noted in the entry.

An asterisk (*) preceding an entry indicates that the species is restricted on the island to the distinctive ephemeral pond and adjacent hardwood swamp habitat near the lighthouse; this habitat, dominated by green ash and a small fringing white cedar swamp, was the richest bryophyte habitat on St. Martin Island (Figures 2 and 3), with twenty-five species present here that are found nowhere else on the island.

Nomenclature, including familial dispositions, follows Flora North America Editorial Committee (2007, 2014) for mosses, and Stotler and Crandall-Stotler (2017) for liverworts. Collections numbers with the prefix “13” are those of Freire alone in 2013, and those with the prefix “14” are those of Freire and Route in 2014. The citation of these collection numbers should also include an “SM” (for St. Martin) prefix; for example, the single collection of *Abietinella abietina* below should be fully cited as “Freire & Route SM14-108.”

MOSESSES

AMBLYSTEGIACEAE

- Amblystegium serpens* (Hedw.) Schimp. 14-39, 14-46, 14-54A. New Delta County record.
- **Campyliadelphus chrysophyllus* (Brid.) R.S. Chopra. 13-37.
- **Campylium stellatum* (Hedw.) C.E.O. Jensen. 14-123.
- **Campylophyllum hispidulum* (Brid.) Hedenäs. 14-6A, 14-54B. New Delta County record.
- **Drepanocladus aduncus* (Hedw.) Warnst. var. *aduncus*. 14-43, also Judziewicz & O’Dell s.n. in 2013.
- **Hygroamblystegium varium* (Hedw.) Monk. subsp. *humile* (P. Beauv.) Vanderp. & Hedenäs. 13-38, 14-48.
- Hygroamblystegium varium* (Hedw.) Monk. subsp. *varium*. 13-61, 14-70C.
- **Leptodictyum riparium* (Hedw.) Warnst. 13-40, 13-45, 14-42, 14-44, 14-50, 14-51. New Delta County record.
- Platydictya subtilis* (Hedw.) H.A. Crum. 13-27B, 13-83B, 14-75A.
- Pseudocampylium radicale* (P. Beauv.) Vanderp. & Hedenäs. 13-26A, 14-45.

ANOMODONTACEAE

- Anomodon attenuatus* (Hedw.) Huebener (A). 13-39, 14-22, 14-63, 14-80, 14-86B.
- Anomodon minor* (Hedw.) Lindb. 14-71, 14-90. New Delta County record.
- Anomodon rostratus* (Hedw.) Schimp. 14-61B, 14-62B, 14-124A.

BRACHYTHECIACEAE

- Brachythecium acutum* (Mitt.) Sull. 13-3, 13-20, 14-59. New Delta County record.
- Brachythecium laetum* (Brid.) Schimp. 14-38, 14-72.
- Brachythecium rutabulum* (Hedw.) Schimp. 14-1. New Delta County record.
- Brachythecium salebrosum* F. Weber & D. Mohr. 13-68, 13-92A. New Delta County record.
- Brachythecium turgidum* (Hartm.) Kindb. 14-73, 14-74, 14-77, 14-86C.
- Eurhynchiastrum pulchellum* (Hedw.) Ignatov & Huttunen. 13-90B. New Delta County record.



FIGURES 2 and 3. Ephemeral pond and green ash hardwood swamp near St. Martin Island lighthouse on July 17, 2013 and August 19, 2014, respectively. The pond, the swamp, and their forested margins have a rich bryoflora. Photos by Emmet J. Judziewicz.

Sciuro-hypnum oedipodium (Mitt.) Ignatov & Huttunen. 13-94, 14-76. New Delta County record.

Sciuro-hypnum plumosum (Mitt.) Ignatov & Huttunen. 14-12A. New Delta County record.

**Tomentypnum nitens* (Hedw.) Loeske. 13-49.

BRYACEAE

Ptychostomum creberrimum (Taylor) J.R. Spence & H.P. Ramsay. 13-11A, 13-12A.

**Ptychostomum pseudotriquetrum* (Taylor) J.R. Spence & H.P. Ramsay. 13-51.

Rhodobryum ontariense (Kindb.) Paris (Bryaceae). 14-41, 14-86A.

CALLIERGONACEAE

**Warnstorfia fluitans* (Hedw.) Loeske. 13-31. New Delta County record.

CLIMACIACEAE

**Climacium dendroides* (Hedw.) F. Weber & D. Mohr. 14-91.

DICRANACEAE

Dicranella heteromalla (Hedw.) Schimp. 14-70A.

Dicranella varia (Hedw.) Schimp. 14-9A. New Delta County record.

Dicranum montanum Hedw. 13-78, 13-80A.

Dicranum polysetum Sw. 14-26.

Dicranum scoparium Hedw. 14-20, 14-90A, 14-91, 14-93.

**Leucobryum glaucum* (Hedw.) Ångstr. 14-102. New Delta County record.

DITRICHACEAE

Ceratodon purpureus (Hedw.) Brid. 13-58, 14-27.

ENTODONTACEAE

Entodon seductrix (Hedw.) Müll. Hal. 14-87. New Delta County record.

FISSIDENTACEAE

**Fissidens adiantoides* Hedw. 14-113.

Fissidens dubius P. Beauv. 14-61A.

**Fissidens osmundioides* Hedw. 14-114A.

**Fissidens taxifolius* Hedw. 14-119. New Delta County record.

FONTINALACEAE

**Fontinalis novae-angliae* Sull. 14-93B.

FUNARIACEAE

**Funaria hygrometrica* Hedw. 13-73, 14-120.

HELODIACEAE

Elodium blandowii (F. Weber & P. Mohr) Eckel. 13-19. New Delta County record.

HYLOCOMIACEAE

Hylocomiastrum pyrenaicum (Spruce) M. Fleisch. 14-10. New Delta County record.

Pleurozium schreberi (Willd.) Mitt. 13-4B, 14-106.

Rhytidiadelphus squarrosus (Hedw.) Warnst. 13-34B.

Rhytidiadelphus triquetrus (Hedw.) Warnst. 13-14, 13-34, 13-67.

HYPNACEAE

Herzogiella striatella (Brid.) Z. Iwats. 14-3. New Delta County record.

Herzogiella turfacea (Lindb.) Z. Iwats. 13-95, 14-5, 14-92B.

Homomallium adnatum (Hedw.) Broth. 14-60, 14-78A, 14-83. New Delta County record.

**Hypnum cupressiforme* Hedw. 14-115. New Delta County record.

Hypnum fauriei Cardot. 13-39. New Delta County record.

Hypnum lindbergii Mitt. 14-49.

**Hypnum pratense* W.D.J. Koch ex Spruce. 13-46.

Platygyrium repens (Brid.) Schimp. 13-79, 14-122.

Pylaisia polyantha (Hedw.) Schimp. 14-37B.

Pylaisia selwynii Kindb. 13-34A. New Delta County record.

MNIACEAE

Mnium spinulosum Bruch & Schimp. 13-59, 14-12B, 14-28, 14-95, 14-96, 14-97, 14-107, 14-118.

Mnium thomsonii Schimp. 13-82.

Plagiomnium ciliare (Müll. Hal.) T.J. Kop. 14-17, 14-88.

Plagiomnium cuspidatum (Hedw.) T.J. Kop. 13-24, 13-26B, 13-29, 13-39, 13-87, 14-4A, 14-34A, 14-36.

Plagiomnium medium (Bruch & Schimp.) T.J. Kop. Judziewicz s.n. in 2013, 14-1.

Plagiomnium rostratum (Schrader.) T.J. Kop. 13-86.

**Rhizomnium punctatum* (Hedw.) T.J. Kop. 14-93A, 14-114B. New Delta County record.

NECKERACEAE

Neckera pennata Hedw. 13-27A, 13-76A, 13-83C, 14-93, 14-98.

ORTHOTRICHACEAE

Orthotrichum pumilum Sw. 14-37A. New Delta County record.

Orthotrichum speciosum Nees. 13-75. New Delta County record.

PLAGIOTHECIACEAE

**Plagiothecium cavifolium* (Brid.) Z. Iwats. 14-52.

Plagiothecium denticulatum (Hedw.) Schimp. 14-21.

Plagiothecium laetum Schimp. 14-16.

POLYTRICHACEAE

Atrichum angustatum (Brid.) Bruch & Schimp. 13-65, 13-67, 14-31, 14-35A, 14-69B. New Delta County record.

Atrichum tenellum (Rohling) Sull. 14-29. New Delta County record.

Polytrichastrum ohioense (Renauld & Cardot) G.L. Sm. 13-97, 14-84.

Polytrichum juniperinum Hedw. 14-30, 14-35B.

POTTIACEAE

Syntrichia ruralis (Hedw.) F. Weber & D. Mohr. 13-12B, 13-13B, 13-26C.

Tortella tortuosa (Hedw.) Limpr. 13-13A, 13-23, 14-7, 14-57B, 14-81, 14-94.

Tortula mucronifolia Schrad. Schwägr. 13-s.n. New Delta County record.

Weissia controversa Hedw. 13-6A, 14-109B, 14-112B. New Delta County record.

SEMATOPHYLLACEAE

Sematophyllum subpinnatum (Brid.) E. Britton. 14-70D. New Delta County record.

TETRAPHIDACEAE

Tetraphis pellucida Hedw. 13-12.

THUIDIACEAE

**Abietinella abietina* (Hedw.) M. Fleisch. 14-108.

Thuidium delicatulum (Hedw.) Schimp. 13-10, 13-11B, 13-21, 13-22, 13-69, 14-25.

Thuidium recognitum (Hedw.) Lindb. 13-8.

LIVERWORTS

ADELANTHACEAE

**Syzygiella autumnalis* (DC.) K. Feldberg, Váňa, Hentschel & Heinrichs. 14-117.

BLEPHAROSTOMATACEAE

Blepharostoma trichophyllum (L.) Dumort. 13-80B, 14-67C.

CEPHALOZIACEAE

Cephalozia bicuspidata (L.) Dumort. 13-35B, 13-55B, 13-60A. New Delta County record.

Fuscocephaloziopsis catenulata (Huebner) Váňa & L.Söderstr. 14-67B. New Delta County record.

Fuscocephaloziopsis connivens (Dicks.) Váňa & L.Söderstr. 13-14, 13-47C. New Delta County record.

Fuscocephaloziopsis lunulifolia (Dumort.) Váňa & L.Söderstr. 13-47D. New Delta County record.

Fuscocephaloziopsis pleniceps (Austin) Váňa & L.Söderstr. var. *caroliniana* (R. M. Schust.) Váňa & L.Söderstr. 13-52A, 13-60C. New Delta County record.

CEPHALOZIELLACEAE

Cephaloziella divaricata (Sm.) Schiffn. 14-68B. New Delta County record.
Cephaloziella rubella (Nees) Warnst. 13-47B, 14-67E.

CONOCEPHALACEAE

Conocephalum conicum (L.) Dumort. 14-92.

FRULLANIACEAE

Frullania eboracensis Lehm. 13-27C, 13-56C, 14-11, 14-55.
Frullania inflata Gottsche. 14-75B, 14-82. New Delta County record.

JUNGERMANNIACEAE

Mesoptychia badensis (Gottsche ex Rabenh.) Váňa & L.Söderstr. 13-60B.

LEPIDOZIACEAE

**Bazzania trilobata* (L.) Gray. 13-11, 14-103, 14-104. New Delta County record.

LOPHOCOLEACEAE

Chiloscyphus pallescens (Ehrh.) Dumort. 13-35A, 13-55A, 14-53.
Chiloscyphus polyanthos (L.) Corda. 13-60D, 14-67A, 14-68A, 14-70B.
Lophocolea bidentata (L.) Dumort. 14-67D. New Delta County record.
Lophocolea heterophylla (Schrader.) Dumort. 13-47A, 13-52B, 13-56B, 13-81C, 14-2, 14-4B, 14-69A, 14-112A.
 **Lophocolea minor* Nees. 13-43, 13-81B, 14-105B.

MARCHANTIACEAE

Marchantia polymorpha L. 13-33, 13-96, 14-85.

PORELLACEAE

Porella platyphylla (L.) Pfeiff. 13-83A, 14-23, 14-62, 14-78B, 14-79, 14-100.

PTILIDIACEAE

Ptilidium pulcherrimum (Weber) Vain. 13-53B, 13-64, 13-81A, 14-8, 14-57A, 14-58, 14-109A, 14-110.

RADULACEAE

Radula complanata (L.) Dumort. 13-56A, 13-76B, 13-77, 14-15, 14-99, 14-124B.

TRICHOCOLEACEAE

**Trichocolea tomentella* (Ehrh.) Dumort. 14-105A. New Delta County record.

DISCUSSION

St. Martin Island is only the second island in the Grand Traverse Islands (Michigan and Wisconsin) to be systematically surveyed for bryophytes. Summer Island, Michigan, located 10 km to the northeast of St. Martin Island, is the only other island in the archipelago with a comprehensive bryological survey, which was made on July 16–17, 1968 by Miller and Halbert (1971). They found 95 moss species (vs. 81 for St. Martin Island) and 35 liverwort species (vs. 24 for St. Martin Island) for a total of 130 bryophyte species (vs. 105 for St. Martin Island) on Summer Island, meaning that Summer Island has a bryophyte flora that is 19% greater than that of St. Martin Island (Table 1). However, Summer Island is larger (891 ha) than St. Martin Island (523 ha), and, based on a slope of approximately 0.3 in Great Lakes archipelago plant species-area curves (Judziewicz et al. 2001), Summer Island should have a flora that is 17% richer

TABLE 1. Comparison of bryophyte floras of islands and peninsulas of northwestern Lake Michigan. The regions are listed from north to south. Sources: Delta County, Michigan: Consortium of North American Bryophyte Herbaria (2020) plus new reports presented in this paper; Summer Island: Miller and Halbert (1971); Door County, Wisconsin (Rose, 2019).

Region	Area (ha)	Number of Moss species	Number of Liverwort species	Total
Delta County, Michigan	303,300	150	65	215
Summer Island, Delta Co., Michigan	891	95	35	130
St. Martin Island, Delta Co., Michigan	523	81	24	105
Door County, Wisconsin	124,800	250	37	287

than St. Martin Island. Thus, Summer Island and St. Martin Island have roughly equivalently rich bryofloras. St. Martin Island’s 105 species of bryophytes represent 49% of the 215 species found in Delta County, Michigan (Consortium of North American Bryophyte Herbaria, 2020), and 36% of the 287 species found in adjacent Door County, Wisconsin (Rose, 2019), just to the south.

The west coast of Summer Island has well-developed alvar plant communities, featuring “moss-clogged springs flowing over dolomite pavement” (Miller and Halbert 1971). In this habitat, which is absent on St. Martin Island (both islands were visited by the third author during 1998 and 2013–2014 field work), Miller and Halbert noted the presence of the following, mostly calciphilic, species that are not known from St. Martin Island: *Aneura pinguis* (L.) Dumort., *Aulacomnium palustre* (Hedw.) Schwägr., *Calliergon giganteum* (Schimp.) Kindb., *Cratoneuron filicinum* (Hedw.) Spruce, *Ditrichum flexicaule* (Schwägr.) Hampe, *Drepanocladus polygamus* (Schimp.) Hedenäs, *D. sendtneri* (Schimp.) Warnst., *Hamatocaulis vernicosus* (Mitt.) Hedenäs, *Hylocomium splendens* (Hedw.) Schimp., *Lophozia porphyroleuca* (Nees) Schiffn., *Philonotis fontana* (Hedw.) Brid., *Preissia quadrata* (Scop.) Nees, *Scapania nemorea* (L.) Grolle, and *Sphagnum capillaceum* (Ehrh.) Hedw.; thus, a total of 14 species found only in this unique habitat. Subtracting these 14 species from the total of 130 found on Summer Island gives 116 species and Summer would have a bryophyte flora that is only 5% poorer than St. Martin Island’s total of 105 species—again, factoring in island size.

Thirty species of mosses and ten species of liverworts represent new records for Delta County, and increase that county’s bryoflora from 175 (Consortium of North American Bryophyte Herbaria, 2020) to 215 species.

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**DIATOM COMMUNITY COMPOSITION
WITHIN *OPHRYDIUM* COLONIES IN NORTHERN MICHIGAN
AND THE DESCRIPTION OF A NEW SPECIES OF
ENCYONOPSIS KRAMMER**

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ABSTRACT

Among the diverse group of organisms categorized as algae, there are some common and well understood symbiotic relationships, such as those between protozoa and *Zoochlorella*. However, there are some similar relationships that have received less attention, such as that between the colonial ciliate *Ophrydium* and diatoms. This study investigates this relationship, specifically comparing the diatom communities within *Ophrydium* colonies with those of the water in which they occur. *Ophrydium* and benthic algal samples were collected from three lakes in northern Michigan (Larks Lake, French Farm Lake, and Osmun Lake). Permanent diatom slides were prepared, and the diatom community composition of *Ophrydium* samples and samples from surrounding periphyton in each lake were analyzed and individual algae were counted and identified. A Jaccard Similarity Index suggests that some of the *Ophrydium* samples were more similar to other *Ophrydium* samples than they were to benthic samples from the same lake. When accounting for species relative abundance through the use of the Shannon-Wiener Index, the stark difference in diversity between benthic and *Ophrydium* samples was revealed, indicating much greater diversity in benthic algal samples. This difference in diversity was greatly influenced by one diatom species, which does not appear to have been described in existing literature which is described here as a new species, *Encyonopsis ophrydiensis* sp. nov., and which accounted for 75% to 93% of the diatom species composition in the *Ophrydium* samples. This species showed a preference for the habitat offered within *Ophrydium* colonies and was not identified in any benthic algal samples. Although it shares some similarities with other *Encyonopsis* species, its unique shape and affinity for *Ophrydium* colonies suggest that it is a newly discovered species. Further research is required to understand how the relationship between *Ophrydium* and *Encyonopsis ophrydiensis* sp. nov. evolved and how each organism is impacted by this symbiosis.

Keywords: *Ophrydium*, diatoms, *Encyonopsis*, new species

INTRODUCTION

Algae are a diverse group of organisms that find many unique ways to exploit their environment. One way in which they may achieve this is through symbiotic relationships. Symbiotic relationships of algae with lichens (e.g., Ahmadjian and

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Jacobs 1981) and corals (Muscatine and Porter 1977) are well-known, but other associations, with groups such as amoebae and ciliated protozoa, are less well known. One example of this kind of relationship is the green algae in the genus *Zoochlorella* K. Brandt living within cells of the ciliated genus *Ophrydium* Bory. *Ophrydium* is classified in the order Peritrichida, as they are single-celled protozoa containing endosymbiotic *zoochlorellae* (Woelfl et al. 2010). The most common endosymbiotic *Zoochlorella* species is *Zoochlorella parasitica* K.Brandt (Winkler and Corliss 1965). Within the cell of the protozoa live photosynthetic *Z. parasitica*, which provides the *Ophrydium* with carbohydrates (Sand-Jensen et al. 1997). These protozoa also filter feed on bacteria in order to obtain additional nutrients. The carbohydrates from *Z. parasitica* are used to build a thick mucilage around the protozoa that can combine with the mucilage of other *Ophrydium* cells, thereby forming a large colony. Each individual within a colony is in its own cylindrically shaped tube, or lorica, which prevents the individual from touching the mucilage matrix (Winkler and Corliss 1965). Individuals are attached to each other by scopula, or basal ciliature. The mucilage holding *Ophrydium* loricas together contains diatoms and soft algae, as well as heliozoans, bacteria, rotifers, nematodes, other ciliates, and crustaceans (Duval and Margulis 1995).

Ophrydium spend a majority of its life benthically in oligotrophic lakes and slow creek beds that lack excess chlorophyll a (Woelfl et al. 2010; Oberholster et al. 2010). Eventually they become planktonic once their colony produces enough gases from photosynthesizing *Zoochlorella* to promote buoyancy (Sand-Jensen et al. 1994). Normally, colonies remain benthic, often attached to rocks, plants, and, in northern Michigan, often on the macro alga *Chara*. Sometimes young colonies can be very dense and firm like a glass marble. Older colonies can take on a squashed doughnut shape, in which their width is larger than their height and the center caves in on one side (Oberholster et al. 2010; Winkler and Corliss 1965). This enables the colony to move up and down the water column. Becoming mobile, however, can be risky for the longevity of the colony as it may be destroyed by external disturbances that break the mucilage apart, thereby causing *Ophrydium* individuals to abandon the colony (Sand-Jensen et al. 1994). It is unclear what the fate of the *Zoochlorella* is in these situations.

Individual *Ophrydium* cells can eject themselves from the colony and become free living, using their buccula (or mouth) cilia and locomotor fringe to propel themselves through the water (Winkler and Corliss 1965). Seasonally, the majority of a colony may asexually produce telotrochs, or “larvae,” that bud off from the adult cell and attach to a nearby substrate. This is one of the few times an *Ophrydium* cell becomes free floating and serves as a successful dispersive strategy for the colony (Winkler and Corliss 1965).

Previous research has been conducted on the endosymbiont *Zoochlorella* and their *Ophrydium* hosts, while research into the composition of algal communities, specifically diatoms, within the mucilage of their colonies, is less common. Geitler (1975) explored the algal species found within *Ophrydium versatile*. Czarnecki (1995) added to the existing body of research, contributing data for diatom composition within *Ophrydium* assemblages at Lake Itasca State Park. He concluded that within the *Ophrydium* assemblages of three nearby

lakes, three taxa (*Cymbella* C. Agardh, *Nitzschia* Hassall, *Brachysira* Kützing) constituted 70% of the identified diatom species. However, his data also suggest that there is no significant similarity in diatom community composition within *Ophrydium* between the three lakes studied. *Ophrydium* studies in Massachusetts (Duval and Margulis, 1995) found that diatom communities within *Ophrydium* collected from Hawley and Leverett bog wetlands, contained diatoms within the genera *Navicula* Bory, *Pinnularia* Ehrenberg, *Gyrosigma* Hassall, and *Cymbella*, while also containing coccoid cyanobacteria, and bacteria (Duval and Margulis 1995). *Navicula* dominated the community within the mucilage, while not being the dominant genus in surrounding waters (Duval and Margulis 1995). Reports of *Ophrydium* colonies have recently come from Russia (Bazhenova and Igoshkina 2016), South Africa (Oberholster et al. 2010) and Argentina (Peso et al. 2015).

While there has been some research to determine the common species of diatoms found in *Ophrydium* colonies, little has been done to compare the diatom communities within *Ophrydium* colonies to the surrounding benthic diatom communities. We investigated the diversity of diatom communities within *Ophrydium* colonies, comparing the diatom composition within *Ophrydium* colonies from three lakes in northern Michigan to the surrounding benthic diatom communities within the lake water from which they were sampled. Specifically, we wanted to determine whether diatom communities within *Ophrydium* colonies from different lakes are more similar to each other or are more similar to benthic diatom communities in the surrounding waters. Within the mucilage of *Ophrydium* colonies, we expected to find a different diatom assemblage than within the surrounding waters, and we expected the composition to be more similar between *Ophrydium* colonies than between each colony and the assemblage in the surrounding water.

METHODS AND MATERIALS

Collections

Samples of *Ophrydium* and surrounding benthic algae were collected at three sites in northern Michigan. Larks Lake (45°36'08.3"N, 84°55'42.7"W), located in Emmet County, is a shallow, spring-fed lake with a marl and sand bottom. This 600-acre inland lake has a maximum depth of 9 feet (Tip of the Mitt Watershed Council 2019). French Farm Lake (45°45'09.2"N, 84°45'57.9"W) (Institute for Fisheries Research 2019) in Emmet County is a shallow, 585-acre inland lake with a marl bottom rich in benthic cyanobacteria. French Farm Lake is partially surrounded by wetlands and contains a multitude of habitats including large patches of reeds and patches of lily pads along the shore. Osmun Lake (45°19'33.8"N, 84°23'24.4"W) is a 48-acre inland lake in Cheboygan County with a marl bottom. Most of the lake is less than 4 feet deep, but with a maximum depth of 10 ft (Cwalinski and Newman 2008). Sampling of all three lakes took place between July 11 and July 22, 2019. Each location was visited on a different day and both benthic algal samples and *Ophrydium* samples were collected on the same date from the same lake.

At all sites, benthic samples were collected from the surrounding area near the *Ophrydium* using a baster and placed in two 4-ounce Whirl-Paks, which were transported back to the lab. *Ophrydium* samples were collected by scooping between 10-20 individual *Ophrydium* colonies in two Whirl-Paks at each site. In Larks Lake, *Ophrydium* samples were collected above the sandy bottom near an aggregate of reeds. In French Farm Lake, *Ophrydium* samples were collected from the benthos, above the marl next to an aggregate of lily pads. *Ophrydium* colonies at this location were

exceptionally large, up to 30 cm wide. Finally, at Osmun Lake, *Ophrydium* colonies were collected above the marl bottom underneath lily pads; several of these colonies were planktonic.

In the lab, the two Whirl-Pak benthic samples from Larks Lake were combined into a 1-liter glass beaker up to 100 ml. This process was completed with the benthic samples from French Farm Lake and Osmun Lake, resulting in a total of 3 beakers, each filled with 100 ml of benthic sample from a particular sampling location. To remove organic matter from each sample, leaving a clean diatom media for ease of viewing and identification using a microscope, the following process was completed. Each beaker received 100 ml of 30% hydrogen peroxide followed by the addition of a small amount of potassium dichromate (Van Der Werff 1955). Following an exothermic reaction, each site sample was then transferred into its own 250 ml beaker and filled with deionized water. Over the course of a week, samples were decanted to about 50 ml and refilled with deionized water every 12 hours until colorless. The cleaned diatoms were transferred onto a cover slip and dried on a warming plate. After drying completely, the coverslips were permanently mounted onto glass slides using Naphrax mounting medium.

For the *Ophrydium* samples, we first extracted the *Ophrydium* colonies from their water environment inside of the Whirl-Paks and placed them into petri dishes. We then removed any *Chara* remnants and thoroughly rinsed the colonies with deionized water to remove any algae clinging to the exterior of the *Ophrydium* colonies. This cleaning was done for every site *Ophrydium* sample. *Ophrydium* samples were then separated into three separate 1-L beakers (one for each site). Each sample was then processed to become diatom slides through the same diatom media cleaning and mounting process as the benthic samples. All samples and slides (benthic and *Ophrydium* samples from each location) have been accessioned into the Diatom Collection of JPK at COLO.

Samples were analyzed with an Olympus BX-51 compound microscope with a 100× objective and DIC optics with a numerical aperture of 1.4. To determine the structure of the diatom communities present in each of the six samples, 600 valves were identified and enumerated. For SEM microscopy, cleaned material was air-dried onto 18 mm round cover glasses, which were then attached to aluminum stubs with double-sided tape. The stubs were sputter coated with 1 nm gold using a Cressington 108 sputter coater (Cressington Scientific Instruments Ltd., Watford, UK). Materials were examined using a JEOL JSM 7401 field emission SEM (JEOL Ltd., Tokyo, Japan) at an acceleration voltage of 3 kV.

Comparison of Communities

To assess the similarity between samples, we calculated Jaccard Similarity Index values (Jaccard 1912). Additionally, a Shannon-Wiener Index of diversity (Spellerberg and Fedor 2003) was calculated to assess the diatom composition of the samples. Again, all species counted from each location and each sample type were included.

RESULTS

Overall, 85 taxa from 39 genera of diatoms were identified from the six samples from the three lakes (Table 1). The number of taxa in each of the 600 valve counts ranged from 13 (*Ophrydium* colonies from French Farm Lake) to 60 (benthic sample from French Farm Lake). The number of taxa from *Ophrydium* colonies averaged 14.6 taxa/sample, while the number of taxa from benthic samples averaged 43.3 taxa/sample. The *Ophrydium* samples were dominated by an *Encyonopsis* species comprising from 75% to just over 93% of the community from *Ophrydium* samples. This species of *Encyonopsis* was not encountered in any of the benthic samples surrounding the colonies. While this *Encyonopsis* species was unique to the *Ophrydium* diatom communities, it was the only species unique to those communities. The benthic communities had 39 taxa that were unique to these communities, that is, not found in the *Ophrydium* samples.

TABLE 1. List of diatom taxa collected from Larks Lake, Osmun Lake, and French Farm Lake and the number of each from a 600-valve collection from each of two substrate types in each lake.

Taxa	Larks Lake		Osmun Lake		French Farm Lake	
	<i>Ophrydium</i>	Benthic	<i>Ophrydium</i>	Benthic	<i>Ophrydium</i>	Benthic
Achnanthidium deflexum						13
Achnanthidium macrocephala						4
Achnanthidium minutissimum	4	74		12		55
Achnanthidium rosenstockii		5				6
Adlafia bryophila			4	16		4
Amphipleura pellucida					2	2
Amphora ovalis		2				2
Amphora thumensis						6
Aneumastus tuscula						2
Brachysira vitrea	2	12	5	93	4	12
Caloneis silicula						2
Cocconeis placentula		5				
Cyclotella comensis	2					8
Cyclotella distinguenda						3
Cymbella affinis		2		6		10
Cymbella hustedtii				2		
Cymbella leptoceros			48	93		
Cymbopleura amphicephala		2				
Cymbopleura cuspidata						4
Cymbopleura naviculiformis					2	2
Cymbopleura subaequalis		2				
Delicataptychus delicatula		4	4	62		
Encyonema minuta		10	2	2		2
Encyonema muelleri						
f. ventricosa		1				
Encyonema norvegica						12
Encyonema sp.				4	2	
Encyonopsis cesatii		24		32	2	
Encyonopsis descripta				4		1
Encyonopsis falaisensis		8		2		
Encyonopsis microcephala	6	82	4	38		52
Encyonopsis ophryidiensis	545		452		559	
Encyonopsis subminuta			18	53		
Eolimna minima		2				2
Epithemia adnata		2				
Epithemia argus		2	6	4		2
Epithemia zebra						2
Eucocconeis flexella		10		12		2
Eucocconeis laevis	2	8				
Eunotia flexuosa		4				
Eunotia implicata	2	6	2	6		
Eunotia sp. 1						2
Fragilaria capucina		4				
Fragilaria sp.		6	2	4	10	
Fragilaria tenera						35
Fragilaria vaucheriae			2	4		
Frustulia rhomboides						1
Gomphonema affine		2				4
Gomphonema intricatum	11	93	2	2		35
Gomphonema sp.		2				
Gomphonema truncatum				2		

(Continued on next page)

TABLE 1. (Continued).

Taxa	Larks Lake		Osmun Lake		French Farm Lake	
	<i>Ophrydium</i>	Benthic	<i>Ophrydium</i>	Benthic	<i>Ophrydium</i>	Benthic
Halamphora perpusilla		2				8
Halamphora veneta						2
Karayevia clevei						1
Lindavia radiosa						18
Mastogloia lacustris	4	2	1	5	1	1
Mastogloia smithii		4				7
Navicula cryptocephala				4		
Navicula hasta						2
Navicula oblonga		2				5
Navicula radiosa	8	85	8	38	4	6
Navicula schadei						8
Navicula sp. 2						2
Navicula trivialis	2	12		10		11
Navicula veneta	8	103	24	64	3	58
Neidium ampliatum		4		4		4
Nitzschia brunoï		2				
Nitzschia denticula	2	4	16	15	8	58
Nitzschia palea				3	2	
Nitzschia sp.	2					4
Nitzschia tenuirostris						9
Pinnularia microstauron						4
Pinnularia sp. 2						2
Placoneis clementis					1	
Planothidium lanceolatum						2
Rhopalodia gibba		2		2		
Sellaphora pupula						6
Stauroneis anceps						4
Stauroneis phoenicenteron						6
Staurosira construens						75
Staurosirella martyi						2
Surirella sp. 1						2
Surirella sp. 2						2
Tabellaria fenestrata		3				
Tabellaria flocculosa						2
Ulnaria ulna		1				2
Unidentified Naviculoid Diatom				2		
TOTALS	600	600	600	600	600	600

The benthic samples were not only more species-rich than the *Ophrydium* samples, but they were also more diverse, as measured by Shannon-Wiener Index. The *Ophrydium* samples had a range of Shannon-Wiener diversity values from 0.401 to 1.095 (average 0.672), while the benthic samples had a range from 2.67 to 3.25 (average 2.86).

The Jaccard's Similarity Index values for the matrix of samples analyzed are given in Table 2. Interestingly, the *Ophrydium* communities were more similar to one another than they were to the benthic communities taken from the same lake, or other benthic communities taken from other lakes. This was the case for both the Lark's Lake *Ophrydium* sample and the French Farm *Ophrydium* sample. In

TABLE 2. Jaccard’s similarity values for cross-sample comparisons between benthic and *Ophrydium* colonies in each of the three lakes.

	Larks Lake		Osmun Lake		French Farm Lake	
	<i>Ophrydium</i>	Benthic	<i>Ophrydium</i>	Benthic	<i>Ophrydium</i>	Benthic
Larks Lake						
<i>Ophrydium</i>	1					
Benthic	0.262	1				
Osmun Lake						
<i>Ophrydium</i>	0.410	0.272	1			
Benthic	0.286	0.373	0.500	1		
French Farm Lake						
<i>Ophrydium</i>	0.285	0.156	0.304	0.257	1	
Benthic	0.159	0.282	0.136	0.200	0.104	1

the case of Osmun Lake, however, the *Ophrydium* sample was more similar to the benthic sample from that lake than the other two *Ophrydium* samples.

While the *Ophrydium* samples had lower species richness, diversity, and far fewer unique species as compared to the benthic samples, the dominant species in each of the three lakes in terms of relative abundance was a species of *Encyonopsis* that appears to be new to science. We describe this new species below:

Encyonopsis ophrydiensis Mark, McKim, Lowe & Kociolek, sp. nov.

Figures 2–24.

Description: Valves narrowly linear-lanceolate, very weakly asymmetrical to the apical axis, dorsal and ventral margins convex, with apices protracted slightly, narrowly-rounded. Length 17–33 µm, breadth 3.5–5.0 µm. Axial area extremely narrow, no central area evident. Raphe filiform, arched to slightly undulate, with external proximal ends dilated slightly and deflected dorsally. Striae not punctate, radiate, strongly so at the apices, 32–36 / 10 µm in the center, 35–38 / 10 µm at the ends.

Holotype: Slide 216001, in the collection of JPK at the University of Colorado, Boulder (COLO).

Type Locality: Osmun Lake, Cheboygan County, Michigan.

Etymology: The specific epithet “*ophrydiensis*” refers to the habitat of the species on *Ophrydium* colonies.

In the SEM images, the valve exterior is dominated by a distinctly undulate raphe, whose proximal raphe ends are wider (Figures 17–20). The proximal raphe ends are deflected towards the dorsal margin. Distally, the raphe ends are hooked slightly and extend onto the valve mantle (Figure 20). Striae are radiate, strongly so near the apices. Areolae are narrow, linear to barely triangular (Figures 19, 20). Internally, the raphe is straight and continuous across the barely distinguished central nodule (Figures 21, 22). The raphe terminates at the apices as helictoglossae (Figures 21, 22, 24), which are located away from the terminus

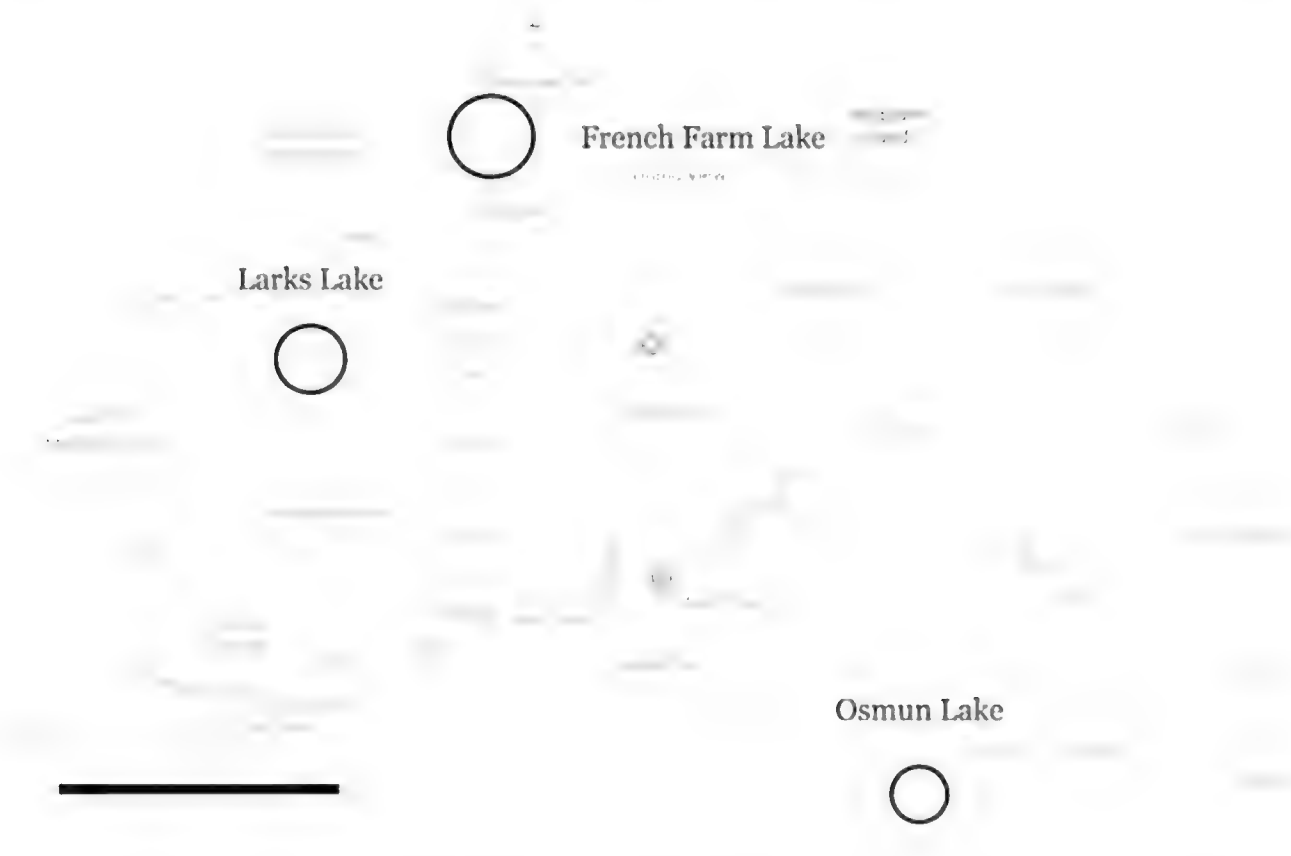
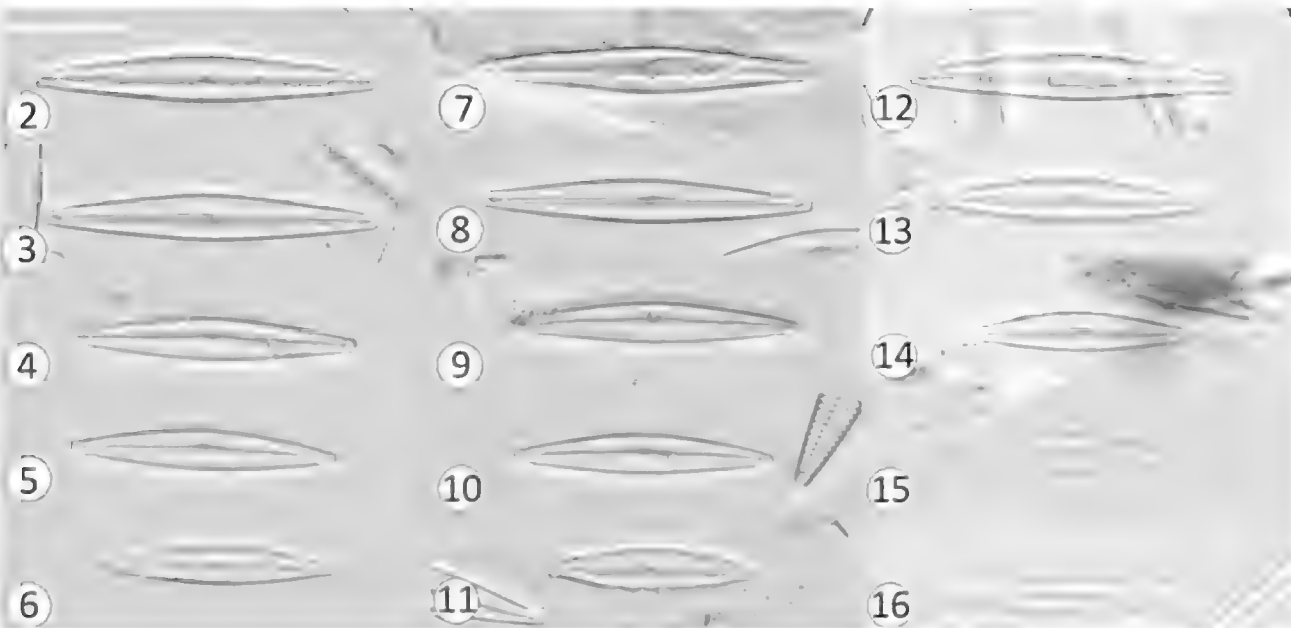


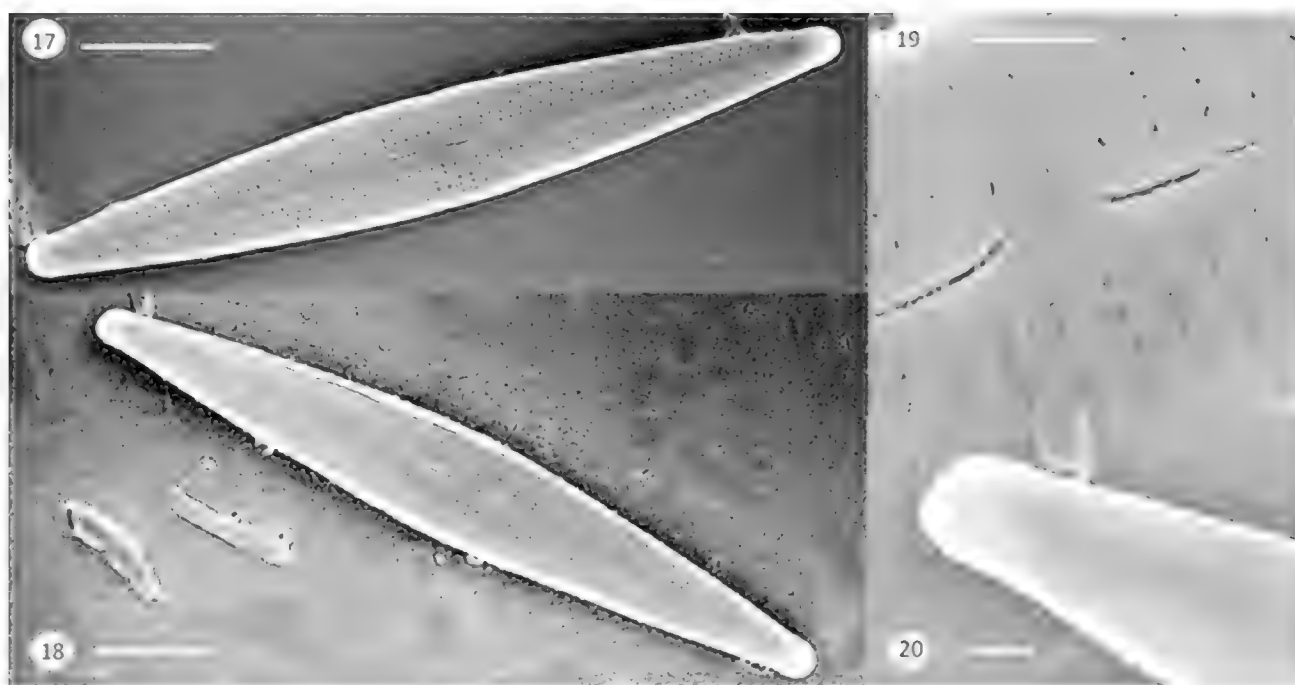
FIGURE 1. Map of the northern Lower Peninsula of Michigan showing the locations of the three study sites. Scale bar = 50 km.

of the valve. Areolae are round openings, located in narrow troughs that are constricted (Figures 21–24).

In his establishment and treatment of the genus *Encyonopsis*, Krammer (1997a) indicated that its diagnostic features include cells that are small, barely asymmetrical, and without apical pore fields and stigmata. Bahls (2015) established the genus *Kurtkrammeria* for those species previously included in



FIGURES 2–16. Light micrographs of *Encyonopsis ophrydiensis* sp. nov. Figures 2–6 are from French Farm Lake. Figures 7–11 are from Osmun Lake (holotype slide). Figures 12–16 are from Larks Lake. Scale bar = 10 μ m for all images.



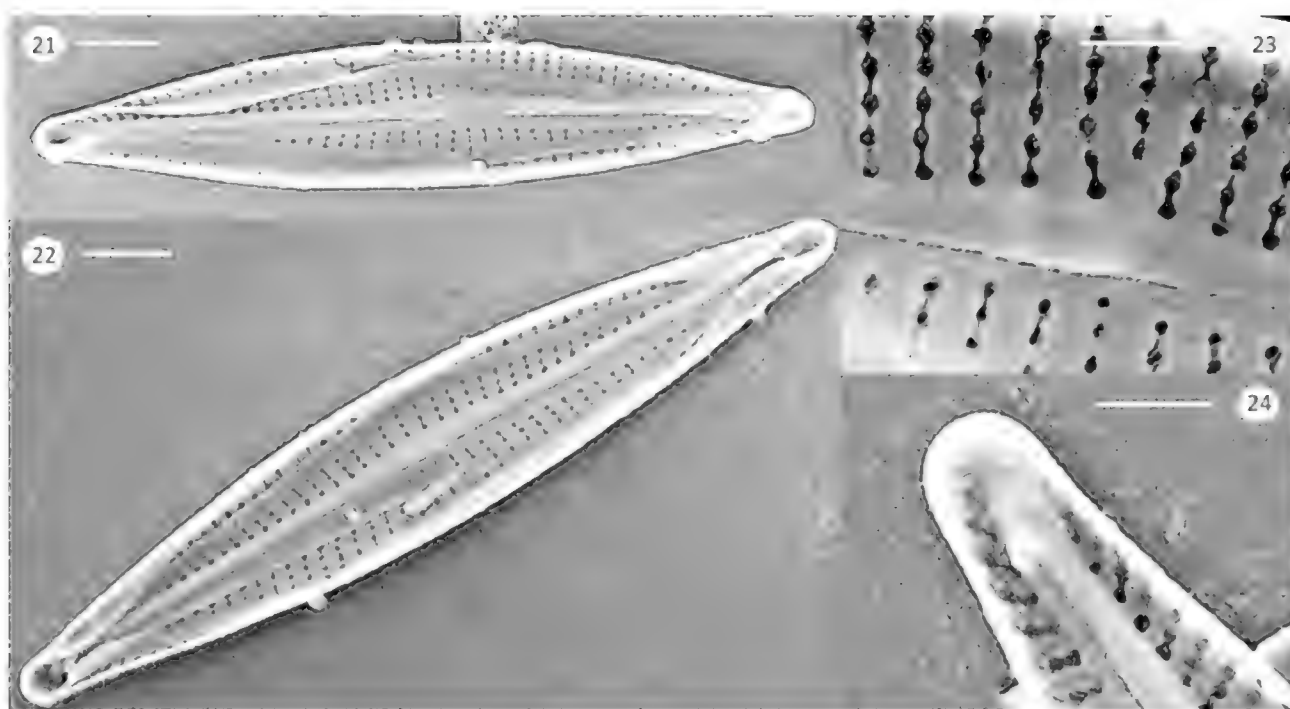
FIGURES 17–20. SEM images of *Encyonopsis ophrydiensis* sp. nov. External valve views. Figures 17 and 18: Whole valve views. Scale bars = 3 μm . Figure 19: Central area, showing proximal raphe ends curved slightly towards the dorsal margin. Areolar openings are small and linear. Scale bar = 0.75 μm . Figure 20: Apex of the valve showing distal raphe end deflected ventrally. Scale bar = 1 μm . All specimens are from Osmun Lake.

Encyonopsis that differ on the basis of the direction of the striae at the apices, the structure of the areolae, and the presence of stigmata and apical pore fields. Lack of these characteristics in the new Michigan taxon places it in the genus *Encyonopsis*.

In his monograph of *Encyonopsis*, Krammer (1997b) considered species from all over the world. There are several taxa that resemble the new species from northern Michigan either in shape or size range. *Encyonopsis delicatissima* (Hustedt) Krammer, *Encyonopsis subruttneria* Krammer, and *Encyonopsis ruttneri* var. *obtusum* (Hustedt) Krammer are all similar in shape to *E. ophrydiensis*, but differ in their smaller length and breadth. All three of these taxa were described originally from Indonesia and, as Krammer suggests, the report by Foged (1959) of *E. delicatissima* from Afghanistan needs verification. The dimensions of those taxa described originally by Hustedt (1938) were confirmed by Simonsen (1987).

Encyonopsis lanceola (Grunow) Krammer has in general a shape similar to *E. ophrydiensis* and similar length and breadth. Grunow's original illustration (in Van Heurck 1880), confirmed in Krammer (1997b, p. 118, Plate 161, fig. 2; Plate 162, figs 1–7) suggests that this species is less asymmetrical to the apical axis than our new species. It had been reported previously from the United States by Patrick and Reimer (1966), but as a species of *Navicula*. This species also has protracted ends that are more broadly rounded than is evident in *E. ophrydiensis*.

Encyonopsis falaisensis (Grunow) Krammer has dimensions similar to those of *E. ophrydiensis*, but the original drawing by Grunow (in Van Heurck 1880) and subsequent light micrographs published by Krammer (1997b, Plate 162, figs 8–24) show that this species does not have protracted apices. Striae density is much coarser (18–20 / 10 μm) (Krammer 1997b) than in *E. ophrydiensis*.



FIGURES 21–24. SEM images of *Encyonopsis ophrydiensis* sp. nov. Internal valve views. Figures 21 and 22: Whole valve. Very thin girdle bands have fallen in to the valve. Straight raphe is evident. Scale bars = 2 μm . Figure 23: Central area, with a slight central nodule, is evident. The raphe is continuous. Areolar openings are round, contained in constricted troughs. Scale bar = 1 μm . Figure 24: Apex of the valve, showing helictoglossa positioned away from end of valve. Striae are radiate. Scale bar = 1 μm . Figures 21, 22, and 24 are from Larks Lake, and Figure 23 is from Osmun Lake.

Encyonopsis ophrydiensis is similar in size and shape to *E. neerlandensis* Van der Vijver (see Van der Vijver et al. 2012), a species found in acid waters of the Netherlands, but also reported from mountain lakes in the Rocky Mountain region (Bahls, 2013). The two species differ in that the species from Michigan may be slightly larger and has finer striae, and in that the species described from the Netherlands has distinctly subcapitate apices.

DISCUSSION

Observations of the diatoms occurring in mucilage of *Ophrydium versatile* show that while the communities in the mucilage of the ciliate are less species-rich and less diverse than those in the surrounding benthic environments, the colonies are quite similar to one another even across lakes separated by nearly 75 km. This suggests that not all species from the surrounding benthic communities are able to survive in the mucilage of *Ophrydium*.

Dute et al. (2000) suggested that the surrounding physical and chemical properties of the water in South Alabama bogs determined the diatom species found in *Ophrydium* colonies there. Since there was only one species unique to *Ophrydium* colonies in the three lakes in northern Michigan investigated here, our data support this general conclusion by Dute et al. (2000). However, the most common species in the mucilage of *Ophrydium* colonies of the three lakes, a new species of *Encyonopsis*, accounted for between 75% and 93% of the entire community present in the colonies and was not encountered in any of the benthic

samples studied herein. This suggests that this species, which forms such a high proportion of the mucilage communities, was able to thrive in these communities relative to the surrounding lake environment and may be an obligate endosymbiont.

The evolutionary relationship between *Ophrydium* and *Encyonopsis ophrydiensis* has not been studied and is especially intriguing in light of the overwhelming high relative abundance of this diatom in *Ophrydium* paired with its absence from the 600 valve counts in the nearby benthic samples. Additional sampling of the benthic waters surrounding the *Ophrydium* colonies may need to be conducted before confidently concluding that *E. ophrydiensis* is obligately found in *Ophrydium*. If this diatom species is found only in *Ophrydium* colonies and not the surrounding environment, it raises many questions concerning the mechanics of how the diatom gets passed on to daughter colonies and how each organism is affected by the relationship (e.g., benefits to *E. ophrydiensis* from living within the *Ophrydium* colony's mucilage).

As noted above, when planktonic *Ophrydium* colonies are disturbed, the *Ophrydium* cells split up and abandon their colony (Sand-Jensen et al. 1994). This raises the questions: (i) when the colonies break, does the *Encyonopsis* species get released into the benthic water or does it remain in the mucilage? (ii) will the *Encyonopsis* species abandon the mucilage if conditions are no longer favorable? and (iii) how does *E. ophrydiensis* remain in the colony if the probability of the colony splitting due to external factors is high? Additional research on the evolutionary relationship between *Ophrydium* and *Encyonopsis ophrydiensis* will contribute to our knowledge of co-evolution concepts as well as mutualistic relationships over time.

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On the cover: Elbow Lake, Elk Township. Much of the shoreline is comprised of exposed marl beds, a highly localized habitat within Lake County, Michigan. Over 30 county records were collected from this area, including several calciphiles such as *Eleocharis rostellata* (spike-rush) and *Berula erecta* (water-parsnip). Photo by B. S. Slaughter, August 21, 2014.